DISSERTATION

GUIDING CONSERVATION OF GOLDEN EAGLE POPULATIONS IN LIGHT OF EXPANDING RENEWABLE ENERGY DEVELOPMENT: A DEMOGRAPHIC AND HABITAT-BASED APPROACH

Submitted by

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ABSTRACT

GUIDING CONSERVATION OF GOLDEN EAGLE POPULATIONS IN LIGHT OF EXPANDING RENEWABLE ENERGY DEVELOPMENT: A DEMOGRAPHIC AND HABITAT-BASED APPROACH

Golden eagles (*Aquila chrysaetoes*) are an iconic wide-ranging predator distributed across the Northern Hemisphere. In western North America, populations are considered to be stable, though there is a mounting concern that an anticipated increase in renewable wind energy development will threaten populations. Wind turbines are a known source of mortality for many avian species including golden eagles, thus there is a pressing need to offer land managers conservation planning guidance in light of future development. Working with several collaborators, I aimed to develop applied research in support of golden eagle conservation, while thoroughly testing the analytical rigor of methods we employed to address such questions.

In chapter 1, I developed a stochastic population model for golden eagles with coauthors Zack Bowen, Brad Fedy, and Barry Noon. We sought to develop a model that faithfully captured the population dynamics of a non-migratory golden eagle population in western North America, while accounting for the demographic and environmental (process) variation inherent in vital rates. Using data from multiple long-term studies, we parameterized a stage-based matrix projection model and evaluated the contribution of vital rates to asymptotic population growth rates within a life-stage simulation analysis (LSA) framework. With a life history that is characterized by long-lived individuals with relatively low reproductive output, breeding adult survival dominates population dynamics for golden eagles. Thus it is unfortunate that breeding

adult survival is the least-represented vital rate estimated in published literature. Simulating reduced survival across stage-classes revealed that a relatively minor (4%) reduction in survival resulted in a growing population to decline. Furthermore, targeting management at bolstering reproductive output is unlikely to compensate for reduced survival. Productivity rates (young fledged per pair) necessary to produce stable asymptotic growth rates (λ=1), when survival is reduced below 4% often falls above the range observed in field studies. Our findings combine to suggest that mitigating for eagle "take" (mortalities) due to anthropogenic sources including wind development should focus disproportionately on strategies that improve survival among breeding adults.

Chapter 2 provides a spatially explicit framework for conservation planning and mitigation for golden eagles with respect to wind development. Co-advisor Brad Fedy and I fit resource selection functions (RSF) to golden eagle nest site data across two major ecoregions across Wyoming. Terrain indices, spatial surrogates for prey density, and landcover explained variation in nest-site locations compared to the available landscape. Overlaying predictive models of golden eagle nesting habitat with wind energy resource maps allowed us to highlight areas of potential conflict among eagle nesting habitat and wind development. Our results suggest that wind potential and the relative probability of golden eagle nesting are not necessarily spatially correlated, revealing opportunities for conservation practitioners and industry to collaborate on energy siting and mitigation strategies.

While these models are useful for conservation planning during a critical life stage in which many eagles are tied to breeding territories, Chapter 3 provides a critical examination of the transient nature of range dynamics during a non-breeding season. Using golden eagle survey data from annual flights across the western US, coauthors Zack Bowen, Brad Fedy, Barry Noon,

and I investigate how climate, anthropogenic disturbance, and ecosystem processes converge to influence late summer space use by golden eagles. We found that spatially invariant processes of Gross Primary Productivity and drought severity drive occurrence patterns, while human footprint and terrain ruggedness are more permanent features that explain variation in space use. Our predictive models are helpful for prioritizing conservation efforts for golden eagles, but underscore the large landscapes necessary for conservation for this wide-ranging species.

Lastly, in Chapter 4 I worked with colleague Travis Gallo using simulation via a "virtual ecologist" framework to evaluate the potential for misleading inference when applying occupancy analyses to point count data, an increasing common trend particularly in avian research. We found that arbitrary decisions about the scale of sites (e.g. sample units) can lead to highly biased estimates with poor coverage across methodological approaches, especially for species with low detectability. Furthermore, varying patterns of detectability can obfuscate community inference –a common among avian point counts. We applied findings to an empirical dataset of songbird response of habitat-treatments targeted for mule deer (*Odocoileus hemionus*) in pinyon-juniper landscapes in northwestern Colorado.

ACKNOWLEDGEMENTS

I thank my co-advisors, Barry Noon and Brad Fedy for accepting, and mentoring me as a student. Brad is a true beacon of pragmatism and style, and provided a compass that always pointed me towards work that was meaningful and interesting. Barry has rightfully earned a reputation as a grand ambassador to the field of conservation; yet, his approach to his work was steeped in a humble and genuine nature that I hope to emulate throughout my career. I am so grateful for the steady wisdom and kind heart that Barry was willing to impart, I am honored to now consider my advisors colleagues.

Colorado State University is full of terrific mentors, and I thank Tom Hobbs and Mevin Hooten for patient guidance and teaching that was critical to my training. I was also fortunate to have a committee that was always sincere in the challenges they presented to me. Randall Boone provided a unique and critical perspective, and Zack Bowen worked hard to offer me opportunities that expanded the scope and utility of my work. Larissa Bailey, simply put, is an archetype of a professional in our field whose intellectual contributions are only exceeded by her good nature.

Life is really all about relationships, and I was fortunate to form many meaningful bonds during my time at CSU. Dr. Noon had assembled an incredible lab of colleagues who I look forward to continuing to work with. Rick Scherer, Helen Sofaer, Jess' Salo & Brauch, and Rehka Warrier were simply *fun* to work with. Pranav Chanchani is destined to make the world a better place for people and tigers, his friendship (and cooking) will always stand out in my mind. Valerie Steen has a depth of compassion that is truly unique. Brian Gerber, Travis Gallo, Lani

Stinson, Joe Northrup, and Perry Williams were steady reminders that ideas, and beer, are best shared with friends.

Lastly, my most rewarding experience at CSU was having the opportunity to meet my wife, Kristen. My training at CSU will help me pursue a life that I am proud, while Kristen constantly reminds me of what makes life beautiful. I dedicate this work to her, and my family.

TABLE OF CONTENTS

Chapter 1: No Substitute for Survival: Life-stage simulation analysis of a golden eagle population model reveals limits to managing for take.

INTRODUCTION

As human domination continues to expand on the earth's ecosystems (Vitousek et al. 1997), a grand challenge for biodiversity lies in conserving populations of animals characterized by high survival and low reproductive output. Long-lived vertebrates with a slow life history, characterized by low annual reproductive output, are most at risk to stressors that lay outside their evolutionary experience (Congdon et al. 1994). In particular, these slow life history wildlife populations exposed to persistent disturbance that results in increased mortality will struggle to support stable population growth, and are most vulnerable to extinction (Webb et al. 2002). This is troubling given the alarming advance of agents that elevate extinction risk including habitat loss and fragmentation (Purvis et al. 2000), spread of invasive species (Gurevitch and Padilla 2004), and global climate change (Thomas et al. 2004). Adding to concern is that these factors disproportionately elevate the extinction risk for large, wide-ranging predators, whom play critical roles in functioning ecosystems (Ripple et al. 2014). Management actions that target the most critical vital rates of slow life history species will be critical in conserving these populations.

Stage-based population models are perhaps the most widely used tool in ecological research to estimate population viability and to gain insights into those management practices most likely to achieve conservation objectives (Caswell 2001, Mills 2012). Properties of simple population projection matrices include information on long-term (asymptotic) population growth

rate, contribution of individual vital rates (e.g., reproduction, survival) to population growth, and a population's expected future st(age) distribution. Because demographic rates are often highly variable, driven by demographic and environmental stochasticity and individual heterogeneity, stochastic population models often most reliably inform management and conservation decisions (Morris and Doak 2002, Lande et al. 2003). Incorporating vital rate uncertainty into population projection models is essential to reduce the likelihood of faulty inference that can arise when these rates are assumed to be constant (White 2000). Life-stage simulation analysis (LSA; Wisdom et al. 2000) provides a framework for evaluating how variation and covariation in life-history traits affects population growth. These analyses, based on the analytical sensitivity and elasticity of individual vital rates, explore changes in growth rate over the realized range of demographic conditions experience by actual populations. Furthermore, characterizing vital rates by probability distributions that reflect true process variance (i.e. heterogeneity arising from demographic and environmental processes; Mills, 2012), lends insight into the ability of management to exploit the plasticity observed in life history traits to increase population level fitness.

Golden eagles (*Aquila chrysaetoes*) are a wide-ranging species of considerable conservation interest that embody the attributes of a slow life-history. Adult eagles can live > 30 years, while mature pairs ($\geq$ 5 years) average fewer than 1 young fledged per year (Kochert et al. 2002). Golden eagles span diverse habitats across all continents in the Northern Hemisphere, yet local populations among this widely distributed species often share common threats (Kochert et al. 2002). Starvation and poor productivity are natural outcomes that arise following adverse environmental conditions affecting prey abundance, for example, yet human-induced sources of mortality currently dominate threats to most golden eagle populations (Watson 2010).

Retaliatory persecution as a response to livestock depredation persists among eagles despite protections provided by federal governments (Beecham and Kochert 1975, Whitfield et al. 2004). However, it is inadvertent human actions that make up the majority of anthropogenic threats to golden eagles (Watson 2010). Golden eagles are subject to collisions with vehicles (Loss et al. 2014), blood-poisoning following lead ingestion (Craig et al. 1990), and electrocution resulting from perching on transmission lines (Lehman et al. 2007). Threats arising from rapid energy development adversely affect the populations of many raptor species including persistence of the endangered Bonelli's eagle (Chevallier et al. 2015). Perhaps the fastest growing threat to golden eagle conservation in North America is that posed by wind turbines used to generate renewable energy (Madders and Whitfield 2006, Kuvlesky Jr et al. 2007, Smallwood and Thelander 2008, Garvin et al. 2011).

In the western US, a recent analysis of population trends supports the inference that populations of golden eagles are stable, though younger age classes may be in decline (Nielson et al. 2014). However, increasing development of wind power is rapidly expanding the human footprint across the North American West (Leu et al. 2008). In particular, the growth of wind power development is likely to outpace that of all other energy sources as the US strives to achieve an energy portfolio composed of 20% renewable sources by 2030 (Kiesecker et al. 2011). This response to increasing energy demands will increase the number of turbines and associated infrastructure including roads and transmission lines (Jones and Pejchar 2013). The focus of our research is to better understand the population-level consequences of increasing mortality rates arising from wind power development in the American West. Confronting stochastic population models with available demographic data provides a framework for investigating potential impacts to populations and provides insights to effective management

strategies. We employed stochastic population modeling in an LSA framework to explore life history sensitivities of golden eagles (*Aquila chrysaetos*) using simulation to develop insights to conservation planning for these slow life-history populations.

Objectives of our research are to: 1) build multiple, stochastic demographic-based matrix models representative of variation in golden eagle demography across western North American; 2) estimate the probability distributions reflecting the process variance inherent in vital rates for golden eagles derived from the published literature; 3) estimate the analytical sensitivity and elasticity of individual vital rates; and 4) examine the ability of increased rates of reproduction to buffer the negative effects of increasing mortality rates. Our models evaluate the demographic consequences of a rapidly increasing human footprint arising from wind power development.

METHODS

Data Collection

We conducted a literature review to identify and compile estimates of golden eagle demographic rates. Our goal was to develop a population model representative of golden eagle population dynamics in western North America. We found surprisingly few estimates of stage-specific survival for any long-lived raptors, including golden eagles. Therefore, we compiled survival estimates for golden eagles, and related 'booted' eagle species across their ranges. To search for published golden eagle vital rates in the peer-reviewed literature, we initiated our search using Google Scholar using search terms "*Aquila chrysaetos*" and "golden eagle", followed by the terms "survival", "nest", "productivity", and "reproduction". We expanded our

search to include government publications, theses and dissertations, and non-governmental organization reports that contained estimated vital rates from golden eagle populations across their range. Only data collected following the ban on dichlorodiphenyltrichloroethane (DDT; 1972 in the US and 1986 in Europe) were considered while all estimates of vital rates from countries where DDT use persists were omitted. This was done to eliminate potential negative biases in reproductive rate estimates.

Constructing a Life-Stage Model

We developed a stage-structured population model for a hypothetical, non-migratory population of mid-continent golden eagles in western North America. Golden eagles exhibit a life stage progression similar to many long-lived raptors—hatchlings → juveniles → subadults (2-4 years old) → adults—with stage classes identified by plumage and molt patterns, while becoming reproductively competent at age 4 as they are entering their fifth year of life (Kochert et al. 2002, Figure 1.1). Breeding adults typically form pairs and begin nest construction or repair during the late winter and early spring, producing 1-2 eggs, followed by approximately 42 days of incubation, with hatchlings emerging late March through early June (Kochert et al. 2002). Hatchlings are dependent upon parental care for approximately two months (45-84d), and fledge during the summer as juveniles. First year juveniles survive to become subadults and remain in this life-stage for three years, which is characterized by distinct molt patterns (Basic I, II, and III) during their 2nd through 4th summers (Bloom and Clark 2001). In their 5th summer, golden eagles will typically obtain definite adult plumage.

Only adults breed in most populations with age of first reproduction occurring at 4-7 years of age (Watson 2010). Subadults occasionally breed but it is uncommon (<2% of nesting

pairs), and may indicate a population with high rates of turnover in adult nesting pairs (Kochert et al. 2002) or a declining population (Ferrer et al. 2003) . Not all adult golden eagles form pairs and initiate nesting—these individuals are colloquially classified as "floaters" (non-breeders). The number of floaters is believed to be density-dependent reflecting the saturation of available nesting territories. Floaters become breeding territory holders following the death of one of the pair or through competitive displacement.

Based on identifiable stage classes, we constructed a six-stage, female-based life cycle graph to describe transitions between juveniles (J), subadults (A_{S1-3}), and adult breeding (A_B) or non-breeding (A_F) golden eagles. Transitions between stages are a function of stage-specific survival probabilities (Figure 1.1). We assume that adults probabilistically transition between nonbreeding and breeding states (γ_{bn}, γ_{nb}), and remain in previous states with complementary probabilities. In addition, we assume a pre-birth pulse 'census' of the population in which fecundity (F) is the product of female productivity (P), 1st year juvenile survival (S_j), and 0.5 assuming equal sex ratios of hatchlings at birth (Rudnick et al. 2005). We equated estimates of nonbreeding adults (or floaters) and subadults survival because these rates (S_{nb}) have been found to be very similar (Hunt and Hunt 2006).

$$\begin{pmatrix} 0 & 0 & 0 & 0 & F & 0 \\ S_{nb} & 0 & 0 & 0 & 0 & 0 \\ 0 & S_{nb} & 0 & 0 & 0 & 0 \\ 0 & 0 & S_{nb} & 0 & 0 & 0 \\ 0 & 0 & 0 & S_{nb}\gamma_{nb} & S_b(1-\gamma_{bn}) & S_{nb}\gamma_{nb} \\ 0 & 0 & 0 & S_{nb}(1-\gamma_{nb}) & S_b\gamma_{bn} & S_{nb}(1-\gamma_{nb}) \end{pmatrix}$$

We expressed the probability distributions of the eagle's vital rates according to their estimated central tendencies and process variation. We assumed a gamma distribution for productivity (P) and estimated the shape of this distribution by fitting a Bayesian gamma regression model to literature-based productivity measures assigning random effects to study site and year (Model details in Appendix 1). Accurate stage-specific estimates of survival estimated for multiple years are uncommon for many long-lived raptors (Sergio et al. 2011) including golden eagles. Thus, limited time series estimates of eagle survival precluded us from fitting a model with random effects to estimate process variation in survival. Rather, we fit a generalized linear model (GLM) with a normal error distribution to logit-transformed survival estimates using a factor covariate to describe variation among stage classes. We used coefficient estimates to obtain means of survival across stages, and used the estimated covariance among model parameters to simulate correlation among survival probabilities following a multivariate normal distribution. We back-transformed randomly sampled values from the multivariate normal distribution to obtain estimates on the scale of survival rates (0-1).

Transition probabilities among breeding states are largely unknown for golden eagles (Kochert et al. 2002), so we set the transition probability from non-breeder to breeding adult (γ_{nb}) so that population growth was deterministically stable ($\lambda = 1$) when other vital rate estimates were held at their mean value. We reasoned that because golden eagle populations in western North America are generally stable (Nielson et al. 2014), deriving transition probabilities to reproduce the observed trends was the most defensible approach for estimating an unknown parameter. Furthermore, we assumed that breeding adults would not transition into a non-breeding state (i.e., $\gamma_{bn} = 0$) and that territory turnover would arise solely from breeding adult mortality (Sánchez-Zapata et al. 2000, Whitfield et al. 2004).

Life-Stage Simulation Analysis

We conducted a LSA by generating k = 10,000 population matrices following random draws from the probability distributions characterizing each vital rate. From each population matrix M_k, we calculated population growth rate as the dominant eigenvalue (λ_k) of the matrix and analytical sensitivity $\left(\frac{\partial \lambda_i}{\partial a_{i,j,k}}\right)$ and elasticity $\left(\frac{\partial \lambda_i}{\partial a_{i,j,k}} * \frac{a_{i,j,k}}{\lambda_i}\right)$ for each vital rate (a). Across all simulations we: 1) individually regressed each vital rate (a_k) on the corresponding estimates of population growth (λ_k) with a linear model, calculating Pearson's correlation coefficient (r^2) to estimate variation in population growth explained by vital rates; 2) calculated the distribution of sensitivities and elasticities across all simulations; 3) for each of the k matrices, ranked each vital rate by the relative magnitude of its sensitivity and elasticity metrics; and 4) tallied the proportion of iterations for which each vital rate held a given rank among the vital rates for each metric.

The expanding wind power energy infrastructure in western North America; which includes transmission lines, roads, and wind turbines; is a source of anthropogenic mortality for golden eagles (Pagel et al. 2013), though it is unclear which age classes or genders are most at risk. One goal of our research was to investigate the possible demographic consequences of additive mortality arising from wind power development in the western U.S. Therefore, we simulated a mean decrease in stage-specific survival rates by proportionally decreasing each survival rate up to 10%, while also including a simulation where survival was reduced equally across all stage classes. For each simulation we calculated asymptotic population growth rate (λ) and the proportion of simulations for which population growth was < 1.0.

Because we were also interested in the ability of increases in reproduction (P) to offset decreases in stage-specific survival rates, we treated reproduction as an unknown across simulations, and derived the value of P such that $\lambda = 1$. We compared simulated values of productivity necessary to achieve a stable population to the observed distribution of productivity by calculating the proportion of simulations that fell within the 95% credible interval of the observed distribution of productivity estimates. This proportion provides insights into the eagle's reproductive potential to realistically offset increased mortality arising from wind power development. All demographic analyses were conducted using the Popbio package in program R (Stubben et al. 2007).

RESULTS

From our literature review, we compiled > 500 records on various aspects of eagle demography. Ninety-eight of the published records of productivity and survival met our criteria for inclusion in estimating the distribution of demographic rates (Appendix 2). The number of productivity estimates was sufficiently large, allowing us to restrict data to those from western North American golden eagle populations (n = 66). Stage-specific survival estimates were rare, requiring us to use estimates from conspecific Bonelli (*Aquila fasciata*) and imperial (*Aquila heliaca*) eagle populations. The estimated shape parameters from the gamma distribution describing productivity estimates were α = 4.80, β = 6.98, yielding an expected (mean) productivity of 0.69 young fledged per pair, with 95% of the support falling between 0.21 and 1.41 young per pair. Survival estimates of 1st year juvenile, non-breeding (subadults and adults), and breeding adults were 0.76, 0.80, and 0.92, respectively. Survival probabilities among juveniles, nonbreeders, and breeding adults all positively covaried. A transition probability from

non-breeder to breeding adult of 0.38 produced stable population growth ($\lambda = 1$) when all other parameters were held at their mean values. Visual inspection of empirical data demonstrated that estimated distributions tracked the range of vital rates sampled in stochastic population models (Figure 1.2).

Life-stage simulation analysis revealed that analytical sensitivity and elasticity were highest for breeding adult survival, followed by non-breeding adult and subadult survival rates (Figure 1.3). Across simulations, breeding adult survival always ranked first with both the highest sensitivity and elasticity values. Similarly, estimates of breeding adult and non-breeding survival explained the most variation in population growth, respectively, followed by productivity, and juvenile survival rate (Figure 1.4).

Reducing survival independently across stage classes from 0 to 10% resulted in disproportionate impacts on asymptotic population growth. Decreasing 1st year juvenile survival up to 10% had only a minor effect on growth rates (Figure 1.5). The proportion of simulations with smaller values of λ rose from 0.56 to 0.63 (Figure 1.6). In contrast, decreasing breeding adult survival by 10% reduced mean λ values from 0.99 to 0.93 (Figure 1.5). Simultaneously reducing survival rates across all stage classes by 4% resulted in > 90% of simulations displaying asymptotic growth rates < 1, while fewer than 1% of simulations resulted in growth rates > 1 following a 7.5% reduction in all survival rates (Figure 1.5).

With no simulated reduction in survival, > 90% of simulations had stable or increasing population growth ($\lambda \geq 1$) with a productivity value included within the 95% credible interval of the empirical distribution of observed values. When survival rates were reduced by 10%, across stage classes < 0.2% of simulations fell within the 95% credible interval of observed productivity

estimates. All simulations with survival decreased by > 4.2% yielded an average value of productivity higher than the maximum observed estimate from the empirical data (1.5 hatchlings per pair to obtain stable population growth; Appendix 2, Figure 1.7).

DISCUSSION

As predicted by demographic theory for vertebrate species with slow life histories (reviewed in Mills 2012:110), population growth rate (λ) is most strongly affected by variation in breeding adult survival rate. Breeding adult survival ranked highest in analytical sensitivity and elasticity across all LSA simulations, and explained the most variation in asymptotic population growth. Simulated declines of 4% in survival across life-stages reduced the ability of populations to exhibit at least stable population growth by 35%. Our findings parallel those of Whitfield et al. (Whitfield et al. 2004), which report that even modest (3-5%) increases in adult survival rates were sufficient to achieve stability in a declining, human-persecuted golden eagle population in Scotland. Limiting non-breeding survival (adults and subadults) had similar, though less pronounced negative impacts on population growth (Whitfield et al. 2004).

Survival among adult breeders is the most important life history attribute affecting the dynamics of golden eagle populations. This finding emphasizes the importance of determining the degree to which wind power development adversely affects adult survival and whether this additional mortality source is acting in an additive or compensatory fashion. Younger, naive eagles may be more at risk to novel stressors, such as electrocution and collisions with wind towers. Further, if wind power development takes place in existing breeding territories, adult golden eagles may also be at risk because they are highly philopatric to these sites. For example,

Chevallier et al. (2015) found that electrocution acted to increase mortality across all life stages of Bonelli's eagles, though younger birds (juveniles) experienced greater mortality. For golden eagles in the western U.S., subadults and non-breeding adults composed all of the mortalities observed at the Altamont Pass Wind Resource Area (Hunt and Hunt 2006). In contrast, a recent synthesis of eagle mortalities across wind farms in the US revealed mortality across all stage classes (Pagel et al. 2013). If wind-power caused mortality is additive to existing sources of mortality, current evidence suggests there is cause for concern.

Increased productivity significantly contributed to golden eagle population growth—42% of the variation across LSA simulations was attributable to reproduction. However, the ability of increased reproductive output to buffer against reduced survival rates diminished quickly with increasing mortality. To achieve population stability, > 50% of simulations with a $\geq 4\%$ decrease in survival across stage classes required productivity to be greater than the maximum observed value. While we did not evaluate the ability of productivity to buffer against stage-specific reductions in loss, we can intuit that loss of breeding adult and non-breeders are most influential. Importantly, productivity, as represented in our population projection models, is actually the combined product of nest initiation probability, clutch size, and nest survival. As a result, it is unclear which components of productivity are most limiting in actual populations.

Our study may not have exhaustively identified all vital rate data for golden eagles and similar species, because many estimates are found in unpublished sources. This was not true for productivity estimates across time and space, as there were several long–term study sites in western North America devoted to monitoring and publishing reproductive success in golden eagle territories (Phillips and Beske 1990, Steenhof et al. 1997, Hunt and Hunt 2006, Mcintyre and Schmidt 2012). In fact, we omitted data from many demographic studies conducted at

nesting sites because productivity estimates were conditional on nest initiation. However, few stage-specific survival estimates were available to us. We found only two estimates of breeding adult survival for golden eagles in western North America, and six range-wide. Emerging tracking technology (Watson et al. 2014, Braham et al. 2015), genetic analyses (Rudnick et al. 2005, Doyle et al. 2014), and use of camera-traps (Katzner et al. 2012) are all promising technologies that should provide improved estimates of these key vital rates. In addition, estimates of transition probabilities among breeding states are difficult to estimate directly, and are most often derived rather than observed (Hunt 1998). Improved estimates of these life-history attributes are needed to reduce the uncertainty in population models used for conservation and management.

MANAGEMENT IMPLICATIONS

Though increases in reproductive output cannot be ignored as part of the conservation portfolio for golden eagles, management that reduces threats to eagle survival should be the top priority, particularly if wind-power development is resulting in increased mortality rates. Our results support the US Fish and Wildlife Services (FWS) mitigation strategy of 'no-net loss' before granting programmatic take permits for proposed wind energy facilities (USFWS 2013). As found for other long-lived vertebrates, variation in adult survival rate is the key demographic parameter affecting eagle population dynamics. Coupling this insight with the fact that > 70% of eagle moralities are linked to human impacts (e.g., vehicle collisions, electrocution along power lines, and poisoning following lead ingestion; Craighead Beringia South, unpublished data), reducing anthropogenic sources of mortality resulting from increased wind energy development

should be a key management objective. For example, electrocution has been a known source of mortality for decades, and despite recommendations to modify transmission line design, exposed power lines remain a pervasive source of eagle mortality (Lehman 2001). Insulating conductors, adding perch deterrents to exposed power lines, or burying transmission lines, are multiple mitigation strategies energy companies could use to lower overall rates of eagle mortality. Modifications to existing transmission lines in areas with high seasonal eagle density, not just those created for new energy development, are also needed to lower mortality rates (Chevallier et al. 2015). Additionally, ungulate viscera discarded by hunters may expose scavengers such as eagles to toxic lead during hunting seasons across North America. For example, Bedrosian et al. (2012) documented elevated levels of lead in bald eagles (*Haliaeetus leucocephalus*) during hunting seasons in Wyoming and the authors found that offering lead-free ammunition to hunters reduced blood lead levels in eagles. Subsidizing the increased cost of lead free ammunition, especially in hunting districts with high density of eagles during the hunting season, may be an effective conservation tool to offset additional eagle mortality rates arising from energy development.

FIGURES

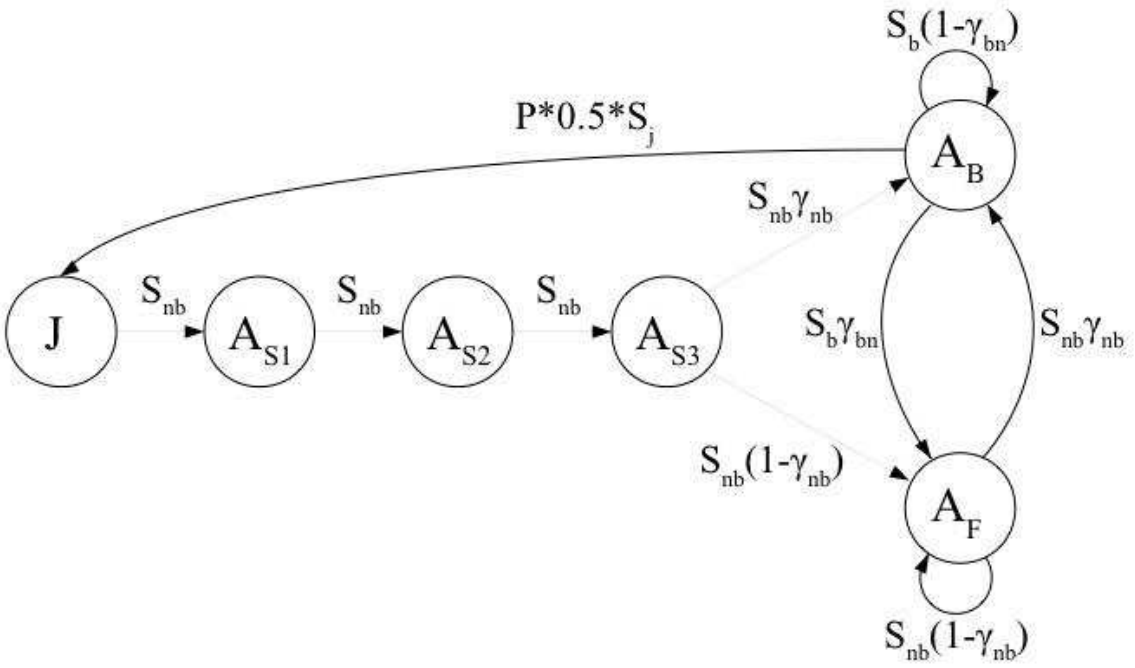

Figure 1.1. Female-based life stage diagram for a hypothetical population of golden eagles in western North America (non-migratory). Juveniles (J; 1 year olds) can survive and transition through three ($\boldsymbol{i}$) subadult phases (A_{Si}). Upon surviving to adulthood, eagles may transition ($\boldsymbol{\gamma}$) between the states of being breeders (A_B) or non-breeding "floaters" (A_F). Only breeding females contribute to future juvenile classes through the product of productivity (P), 1st year juvenile survival (S_j), and 0.5 assuming an equal sex ratio.

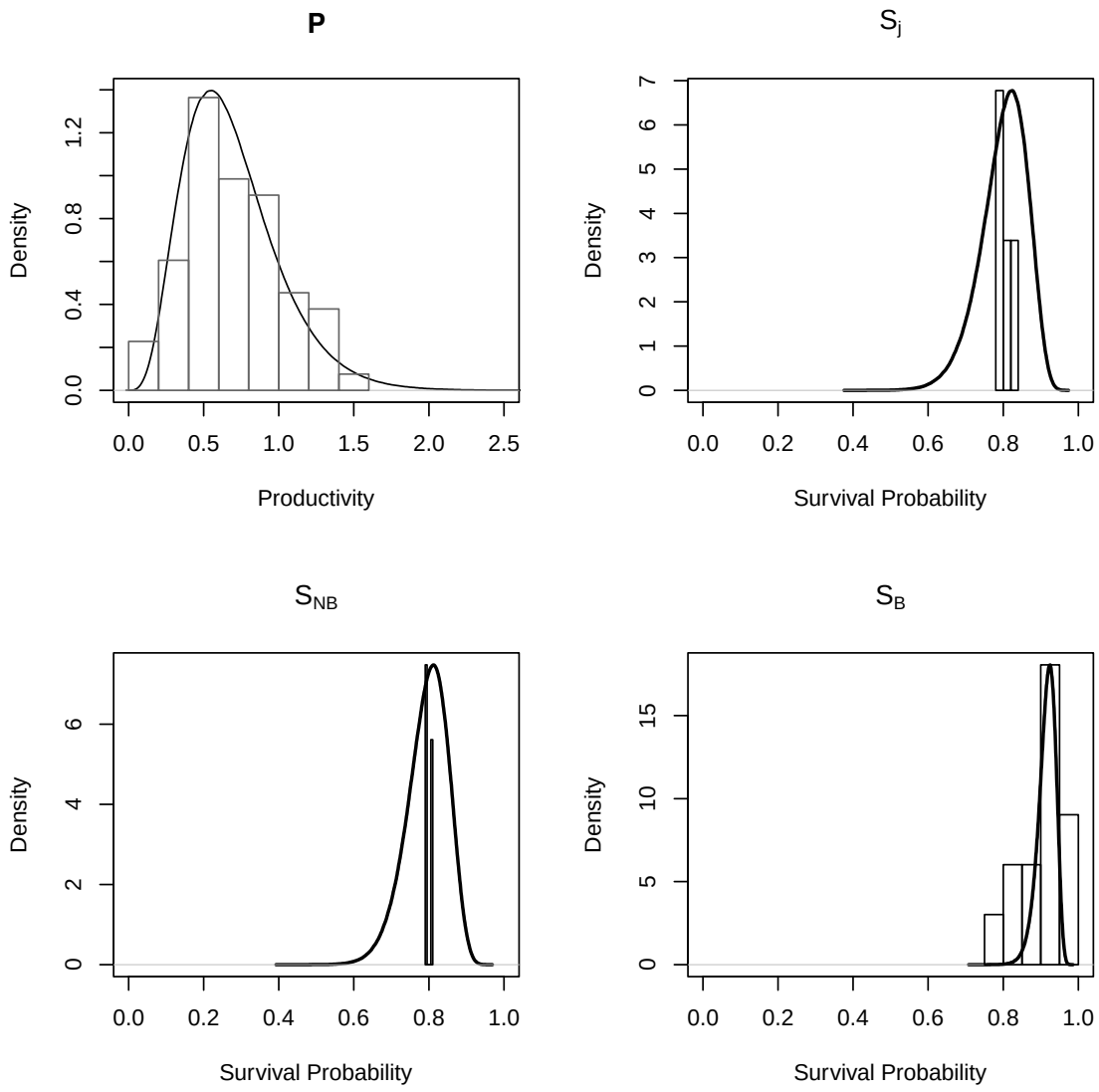

Figure 1.2. Estimated distributions of golden eagle vital rates: productivity (***P***) and 1st year juvenile (***S_j***), non-breeding (***S_{nb}***), and breeding adult (***S_b***) survival based on published estimates of these parameters. Histograms show data compiled to fit the respective distributions.

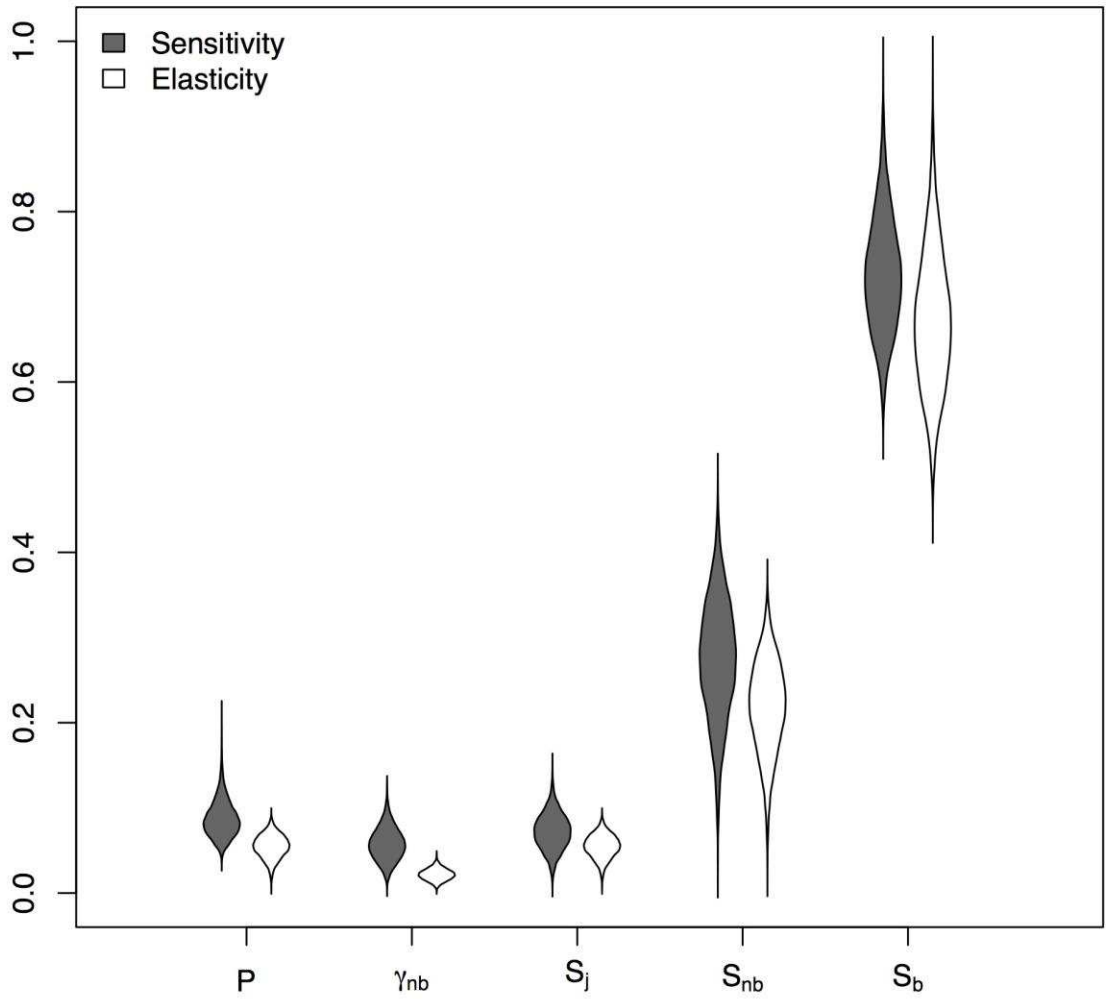

Figure 1.3. Vital rate sensitivity and elasticity estimates for productivity ($\boldsymbol{P}$), transition (non-breeder to breeding adult) probability ($\boldsymbol{\gamma_{nb}}$), and 1st year juvenile ($\boldsymbol{S_j}$), non-breeding ($\boldsymbol{S_{nb}}$), and breeding adult ($\boldsymbol{S_b}$) golden eagle survival.

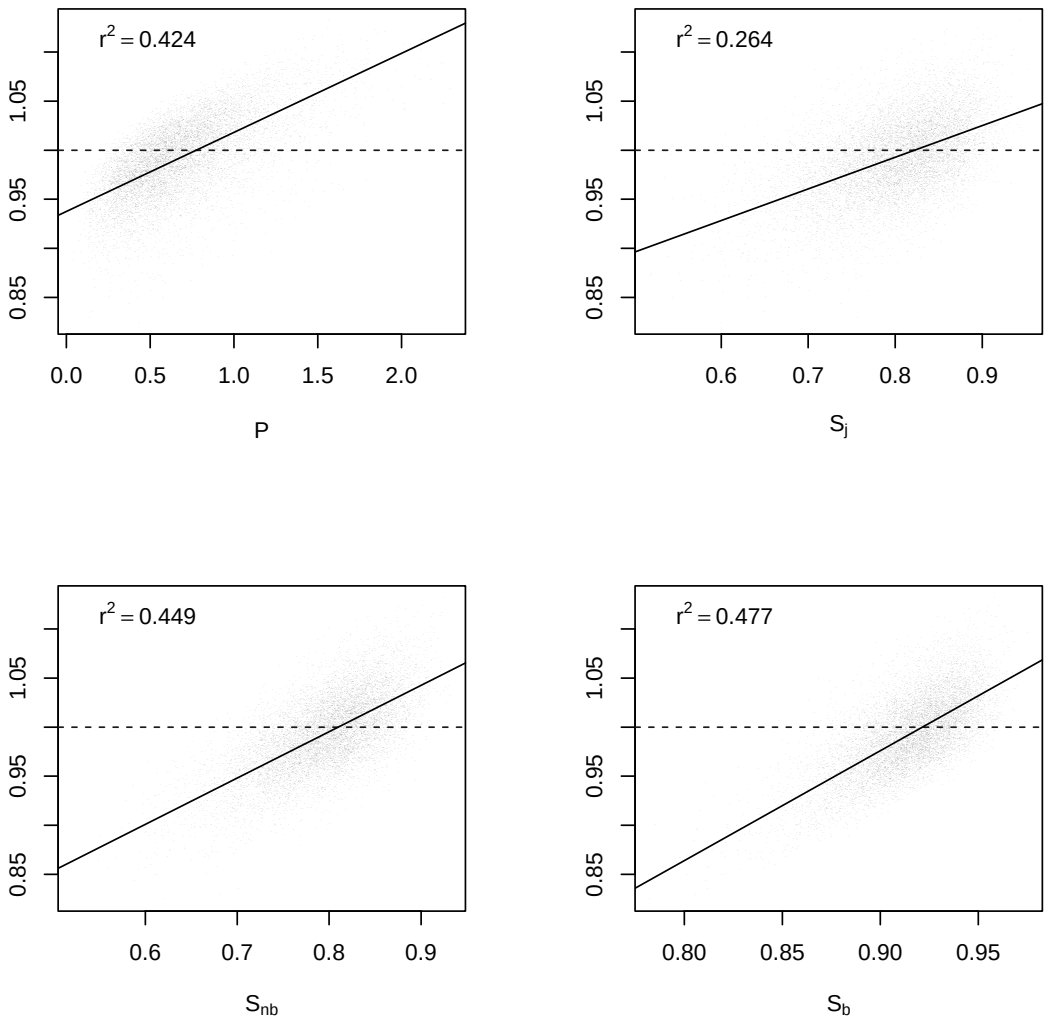

Figure 1.4. Linear regressions of the dominant eigenvalue of simulated projection matrices (population growth rate, λ) on the vital rates considered individually productivity (***P***), and 1st year juvenile (***S_j***), non-breeding (***S_{nb}***), and breeding adult (***S_b***) survival.

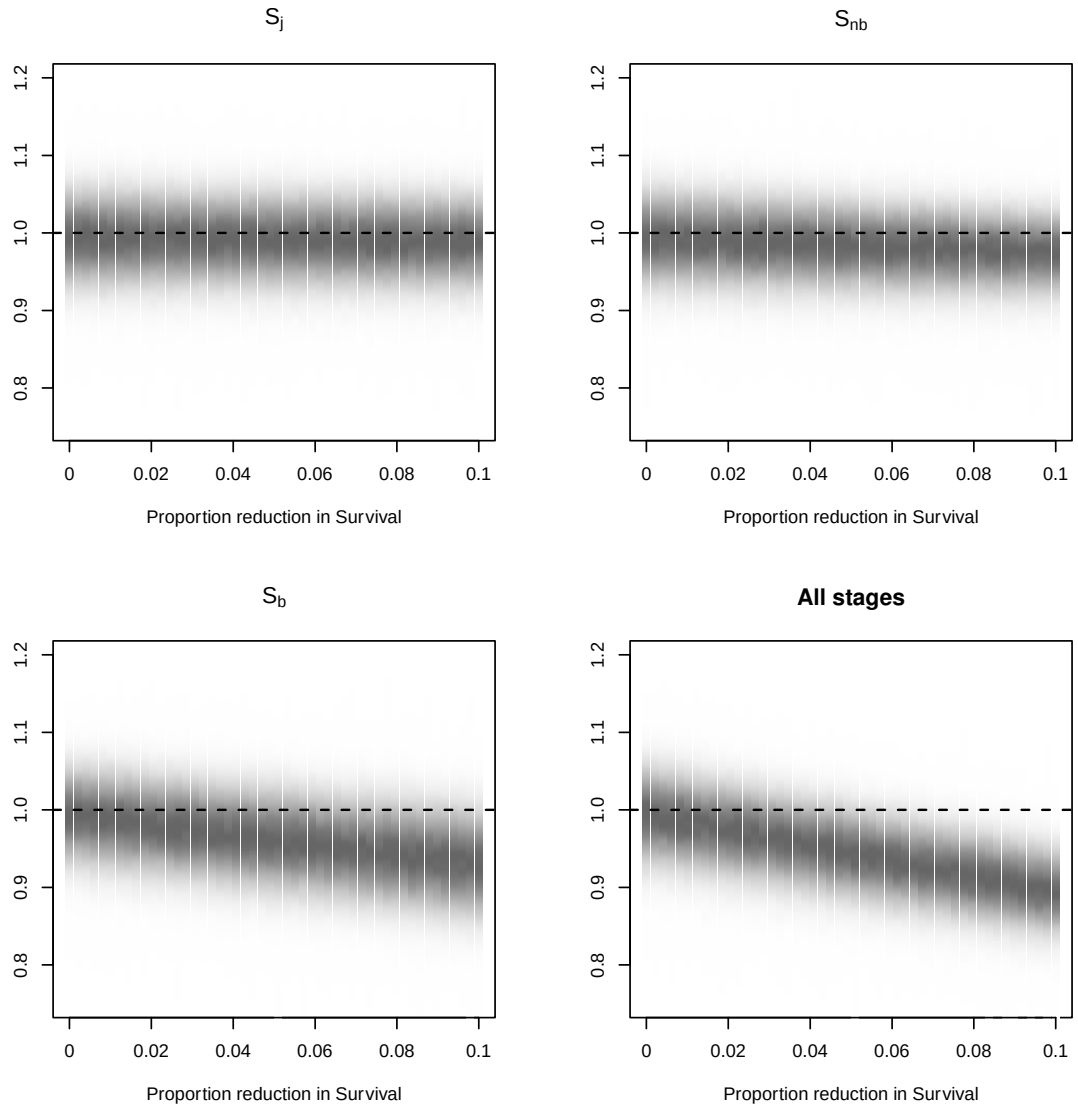

Figure 1.5. Plots of the dominant eigenvalue of simulated projection matrices (population growth rate, λ) on proportional reductions (0 to 10%) in the values of the vital rates considered individually [1st year juvenile ($\boldsymbol{S_j}$), non-breeding ($\boldsymbol{S_{nb}}$), and breeding adult ($\boldsymbol{S_b}$) survival], and across all stages of survival.

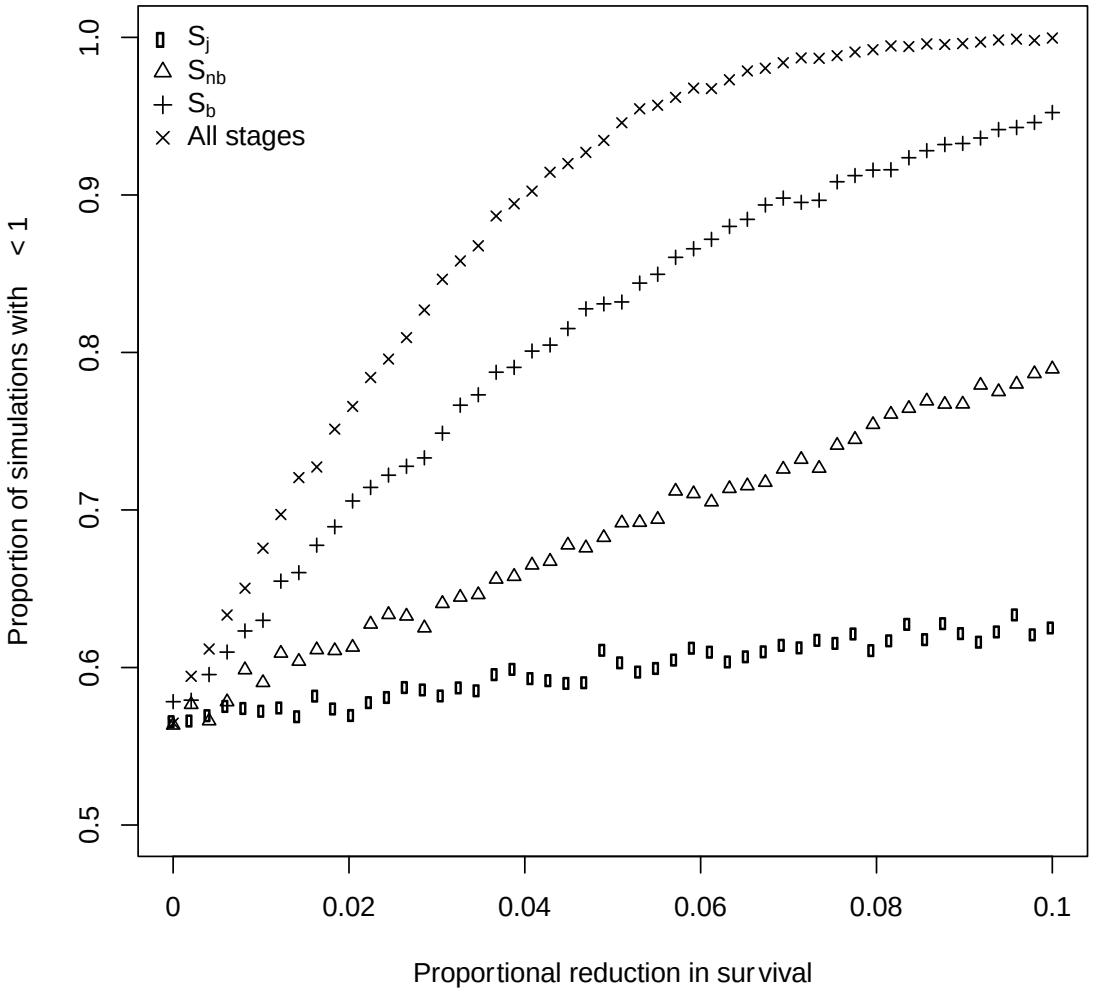

Figure 1.6. The proportion of simulations that resulted in declining asymptotic population growth rates ($\boldsymbol{\lambda} < 1$) following incremental decreases in survival for each stage class including 1st year juvenile ($\boldsymbol{S_j}$), non-breeding ($\boldsymbol{S_{nb}}$), and breeding adult eagles ($\boldsymbol{S_b}$), and across all stages of survival.

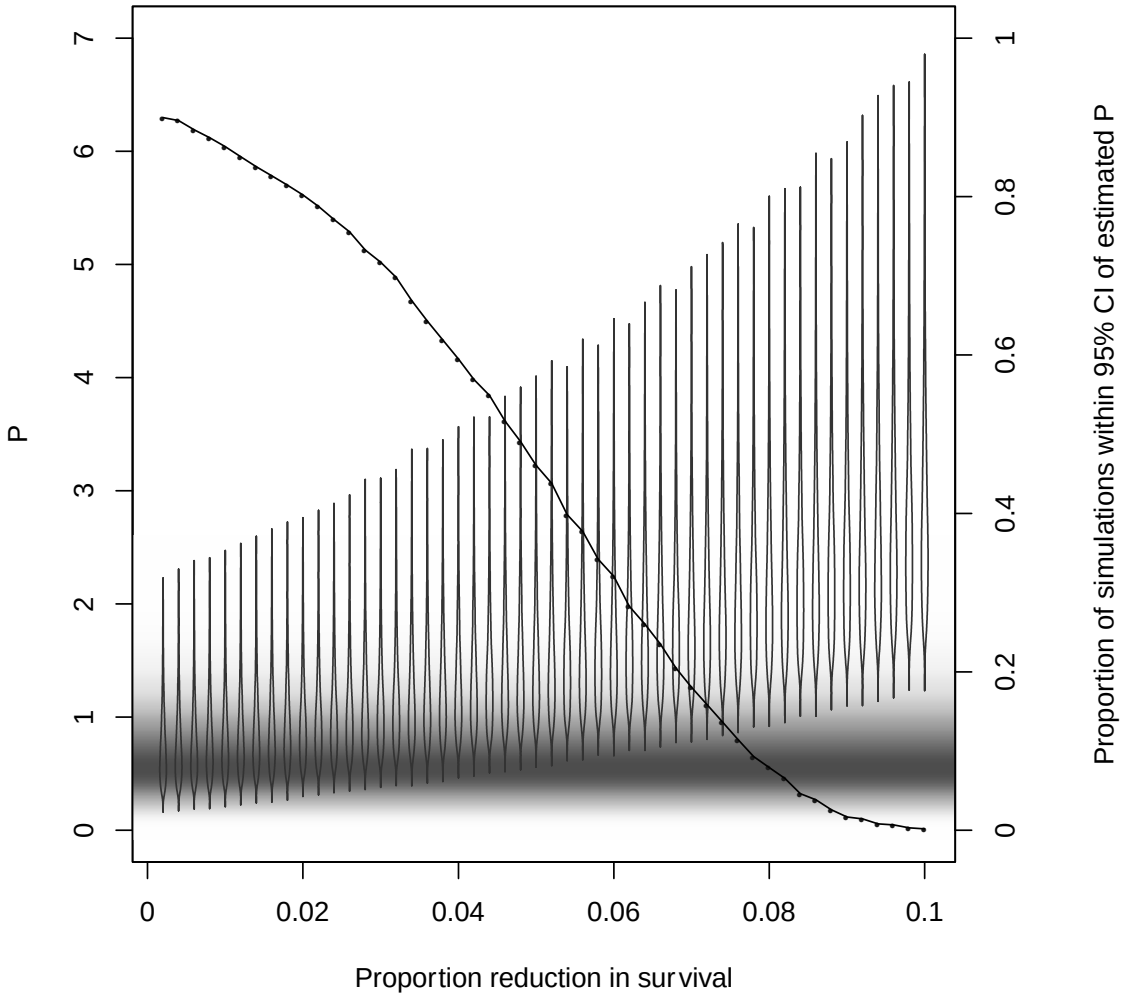

Figure 1.7. Distribution of simulated values of productivity (P; violin plots, y-axis, left) necessary to achieve stable asymptotic population growth ($\boldsymbol{\lambda = 1}$) while simultaneously decreasing survival across all stage-classes up to 10% (x-axis) are displayed. Shaded density strip represents gamma distribution fit to empirical productivity data. Dotted curve is the proportion of derived values of P that fall within the 95% credible interval of the empirical productivity distribution (y-axis, right).

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Chapter 2: Landscapes for energy and wildlife: conservation prioritization for golden eagles across large spatial scales.[1]

Proactive conservation planning for species requires the identification of important spatial attributes across ecologically relevant scales in a model-based framework. However, it is often difficult to develop predictive models, as the explanatory data required for model development across regional management scales is rarely available. Golden eagles are a large-ranging predator of conservation concern in the United States that may be negatively affected by wind energy development. Thus, identifying landscapes least likely to pose conflict between eagles and wind development via shared space prior to development will be critical for conserving populations in the face of imposing development. We used publically available data on golden eagle nests to generate predictive models of golden eagle nesting sites in Wyoming, USA, using a suite of environmental and anthropogenic variables. By overlaying predictive models of golden eagle nesting habitat with wind energy resource maps, we highlight areas of potential conflict among eagle nesting habitat and wind development. However, our results suggest that wind potential and the relative probability of golden eagle nesting are not necessarily spatially correlated. Indeed, the majority of our sample frame includes areas with disparate predictions between suitable nesting habitat and potential for developing wind energy resources. Map predictions cannot replace on-the-ground monitoring for potential risk of wind turbines on wildlife populations, though they provide industry and managers a useful framework to first assess potential development.

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INTRODUCTION

The increasing energy demands of a growing human population pose one of the greatest threats to conserving wildlife populations and their habitats globally (Naugle 2011). Impacts from energy development can negatively affect wildlife through a suite of direct and indirect mechanisms including habitat loss and fragmentation (McDonald et al. 2009, Theobald et al. 2011), increased mortality (Holloran et al. 2010), spread of invasive species (Bergquist et al. 2007), noise pollution (Bayne et al. 2008), and environmental contaminants (Campagna et al. 2011). The negative impacts associated with these processes can have synergistic effects, and the associated risks to wildlife may also be heightened by catastrophic events. The footprint of current energy development is extensive, and will continue to encroach on wildlife habitats. World energy consumption is expected to rise by >25% by 2030, with the highest growth rates of energy supplies coming from renewable sources (Gruenspecht 2010). Developing sources of renewable energy pose a paradoxical challenge to wildlife conservation practitioners. Extracting more energy from renewable sources will curb carbon emissions and potentially slow global climate change to protect the future of wildlife populations and their habitats. However, the infrastructure required for developing and maintaining renewable and traditional energy sources often occurs in disparate areas (Jones and Pejchar 2013). Therefore, renewable energy development has the potential to impact wildlife populations and their habitats in some of the largest intact landscapes that remain outside of areas traditionally developed for energy exploitation.

Wind energy is a potentially important source of renewable energy globally. In the United States, the Department of Energy established a benchmark of generating 20% of the U.S.

electric supply with wind energy by 2030 (http://www.20percentwind.org). This goal will require a dramatic increase in the number of wind turbines throughout the U.S, and the potential effects of large-scale wind energy development on wildlife are not well understood (Pruett et al. 2009). Thus, guidelines for selecting landscapes to minimize the potentially adverse impacts of wind energy on wildlife are a research priority (Fleishman et al. 2011). Proactively identifying areas for resource development with limited potential impact to wildlife is a promising approach to facilitating energy development while maintaining viable wildlife populations across landscapes (Fielding et al. 2006, Bright et al. 2008, Kiesecker et al. 2011).

Golden eagles (*Aquila chrysaetos*) are a widely distributed raptor of conservation concern in North America (Kochert et al. 2002). While many raptor species are potentially impacted by increases in wind turbine development (Hötker et al. 2006), golden eagles are a focal species for conservation planning in the United States due, in part, to federal protection they receive under the Bald and Golden Eagle Protection Act (1963). Wind development projects can displace raptors from otherwise suitable habitat, and are a significant source of mortality when placed in areas with high raptor concentrations (Garvin et al. 2011). For example, Smallwood and Thelander (2008) estimated approximately one golden eagle mortality from collisions with wind turbines per 8.7MW of energy produced annually. This level of mortality is of particular concern for long-lived vertebrates, such as eagles, because even a relatively minor increase in adult mortality (3-5%) can lead to significant population declines (Whitfield 2004).

Wyoming is emblematic of the challenge to balance wildlife conservation and natural resource development. Wyoming is among the top ten energy producers globally with >100,000 producing oil and gas wells and 400 million tons of coal produced annually (http://www.wma-minelife.com/coal/coalfrm/production.htm). Additionally, Wyoming is among the top five U.S.

states in generating electricity from wind power (www.awea.org). The energy-based economy in Wyoming will likely experience continued growth with some of the world's largest deposits of oil and gas reserves (Copeland et al. 2009), and potential undeveloped wind energy (Kiesecker et al. 2011).

Our primary objective was to develop a landscape-level planning tool for golden eagle conservation to be used by resource managers and industry prior to the development of renewable energy. Specifically, we aimed to 1) identify golden eagle nesting sites from available data across Wyoming, 2) develop predictive spatial models of golden eagle nesting occurrence, and 3) identify areas of potential conflict and opportunities for golden eagle conservation in the face of expanding wind energy development. Overlays of predictive nesting habitat maps with maps of potential for wind development explicitly delineated areas of potential opportunity for conservation (high quality habitat, low energy potential), and areas posing conflict between development and nesting habitat (high quality habitat, high energy potential).

METHODS

Study Area

Our sampled population included golden eagle nesting locations across Wyoming, USA. Wyoming encompasses 253,300km^2 of predominately sagebrush steppe habitat at the junction of the Great Plains and Wyoming Basin ecosystems, with intermittent regions covered by the Rocky Mountains. Land tenure in Wyoming is a mixture of private (44%), federal including the U.S. Bureau of Land Management (BLM; 28%) and Forest Service (14%), and state (6%)

ownership. Predominant land uses in Wyoming include cattle grazing, tillage agriculture, and oil and gas energy production.

Data Collection

We requested records from state, federal, non-government, and private entities that collect golden eagle nest data in Wyoming. Access to non-proprietary data resulted in 11,709 records of golden eagle nests between 1974 and 2010. The majority of records were collected between 2000 and 2010 (57%). Records were primarily contributed by the BLM (51%), Wyoming Game and Fish Department (WGFD; 38%), and Thunder Basin National Grasslands (9%). These entities collected location data using a variety of survey methods; including probability-based sampling surveys, mitigation surveys in response to development requests on public lands, and opportunistic sightings. Nest searches included ground-based and aerial methods. We compiled all location data, date of observation, nest status, and source of data. Once the data were compiled, we screened data for consistency in nomenclature and locational accuracy. Any concerns with the data were addressed with the original data managers or censored if irreconcilable problems existed (e.g. uncertainty regarding nest status). The minimum information required for a data record to be included in our analyses was: 1) certainty that the location represented a golden eagle nest (i.e., identification to species level), 2) accurate location data (<120m accuracy), and 3) the year of nesting. Most data had information that could be used to determine the status of the nest following established nomenclature (Postupalsky 1974) as: active (nests in which eggs have been laid), occupied (a nest with adult presence or strong sign of presence), and inactive (a nest with no apparent recent use or adult presence).

Delineating the Sample Unit

The compiled dataset contained records that had considerable redundancy, both within and across nesting seasons. Golden eagle pairs can maintain upwards of 14 nests in a territory (Kochert et al. 2002), and it is likely that groups of nearby nests represent single nesting pairs. Spacing between golden eagle territories (cluster of nests maintained by one pair) varies from 0.8km in southwest Idaho (Beecham 1975) to 44.7km in Quebec (Morneau et al. 1994). Thus, using all nest records in the full dataset for analyses would likely result in pseudoreplication (Hurlbert 1984) by including multiple nests within a single territory. We generated an algorithm that identified and reduced spatially dependent clusters of nests to a single nest site based on a hierarchy by year and nest status, while enforcing a minimum spacing between nest sites of 3km, the mean distance between occupied nests across 12 areas in Wyoming (Kochert et al. 2002). This algorithm minimized underrepresentation of true nest sites available in the sample without proliferating pseudoreplication by treating all nests in the database as independent. To identify nest sites, we first created a data frame of all known nest locations and neighboring nests within 3km. Starting with the most recent year, the algorithm identified each cluster of active and occupied nests to select the nest site with the highest activity level (e.g., 'active' trumped 'occupied'). All nests within 3km of the identified used nest site in that year would then become associated 'alternate' nests, and the algorithm would continue to the subsequent year until no records remained to be classified. If there was >1 record with the same year and status in a cluster (i.e. two nests in 2010 classified as active), then one record was chosen randomly to represent the nest site.

Regional Models

Regional variation in habitat availability can confound habitat selection models if not considered explicitly (Aarts et al. 2008). Landscape features relevant to golden eagle ecology can vary widely across Wyoming, so we developed two regional models to minimize landscape heterogeneity. The North American Commission of Environmental Cooperation (NACEC; 2009) Level II Ecoregional Assessment identifies five distinct ecoregions in Wyoming: The Southern and Middle Rockies, Northwestern Great Plains, High Plains, and the Wyoming Basin. Our aim was to build distinct models for each NACEC level II ecoregion (hereafter, ecoregion), though the majority of golden eagle nest data were contained within the Wyoming Basin (WYB) and Northwestern Great Plains (NWGP) regions. Other regions had insufficient data (<30 used nest sites) to estimate RSFs and were censored from analyses. We focused our analyses on the NWGP and WYB regions in the state, which encompassed roughly 2/3 of Wyoming and contained 95% of available nest data.

Defining Availability

Defining an available sample influences the inference derived from habitat selection models (Jones 2001) and should be conducted at a spatial scale that matches the hierarchical ordering of habitat selection for the sampled unit (Johnson 1980). We constrained random points to within the Wyoming GAP vertebrate primary and secondary distribution for golden eagle, ensuring random points were within habitat potentially suitable for golden eagle nesting (Merrill et al. 1996). We saturated the available landscape with available points at 3km spacing (Northrup et al. 2013). To assign time-specific covariates to available sites, we first calculated the distribution of years represented in nest sites, and randomly assigned a year to each available location based on the proportion of nest sites within that year for each region. This allowed for a

similar distribution of time-stamped covariates to be appended to all points because available samples were temporally-varying at the same frequency as nest sites in each region.

Scale Selection

Measuring biotic and abiotic resources at spatial scales relevant to the ecology of a focal species is critical in understanding patterns of habitat selection (Wiens et al. 1987). Golden eagles demonstrate hierarchical selection for nest sites by choosing suitable cliffs or tall trees locally (Kochert et al. 2002), that are within a landscape of reliable prey base, and terrain conducive to hunting (Watson 2010). Thus, we measured predictor variables at a 200m radius around the nest to capture local-scale attributes associated with nest placement. We also measured predictor variables using a home-range estimate of 3km (Marzluff et al. 1997), and 1 and 5km radii to test hypotheses that golden eagles select for habitat at smaller and larger spatial scales.

Candidate Predictor Variables

We conducted a literature review and consulted experts to develop hypotheses about environmental and anthropogenic features that influence nest site selection by golden eagles. To test hypotheses, spatial predictor variables had to be available across both the NWGP and WYB regions in Wyoming. For several relevant candidate predictors, complete spatial data were unavailable and for these variables we used surrogate measures that were spatially complete. Furthermore, many spatial data layers were indirectly derived from models and have associated measurement errors (Table 2.1).

Prey abundance and availability were identified as the most important components of habitat selection by golden eagles during the breeding season (Maclaren et al. 1988, Marzluff et al. 1997). Golden eagle prey predominately on Leporids in the North American intermountain

West, which comprise up to 70% of their diet during the breeding season (McGahan 1968). There are no spatial data related to the abundance of Leporids in Wyoming, though recent evidence suggests a strong temporal and spatial correlation between the abundance of cottontail rabbits (*Sylvilagus* sp.) and another prey item of golden eagles, greater sage-grouse (*Centrocercus urophasianus;* hereafter, sage-grouse; Fedy and Doherty 2011). Sage-grouse leks (communal breeding grounds) are mapped across Wyoming and almost completely (99%) contained within the golden eagle distribution across the state. Each lek has an associated annual male count that serves as an index to abundance (Reese and Bowyer 2007, Fedy and Doherty 2011). We summed the number of active sage-grouse leks (leks with $\geq$1 male counted in the most recent two years of observation), for a temporally-varying covariate describing the presence of a lek. We used male counts on leks as an index to abundance, generating year specific layers for the regional variation in sage-grouse lek numbers at the largest scale (5km). To build layers we used the maximum male count within years, and when male count data were missing we used the most recent count for generating layers.

Large scale covariates related to climate and primary productivity may also covary with the abundance of golden eagle prey. We extracted annual estimates of precipitation, and minimum and maximum temperature data from PRISM for June (www.prism.oregonstate.edu). We extracted the year specific estimate to each observation with a quadratic term for precipitation, and also included a one year lagged term by appending data from the previous year of an observation. An index of primary productivity was derived from Normalized Difference Vegetation Index (NDVI) from Moderate Resolution Imaging Spectroradiometer (MODIS) data. We averaged NDVI estimates between a typically wet (2007)

and dry (2004) year, and calculated mean and standard deviation of neighborhood values at scales larger than 200m.

Golden eagles typically nest in mid-elevation cliffs (McGahan 1968, McIntyre and Collopy 2006), though they also use ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) in forested habitats of Wyoming (Bryan Bedrosian, Craighead Beringia South, personal communication). Because analyses were constrained to sagebrush and grassland habitats of NWGP and WYB, we hypothesized that eagles would prefer areas of strong topographic relief locally (Phillips et al. 1984). Using a 10m National Elevation Dataset we extracted elevation data, and generated topographic indices to describe cliffs, and other landforms. Using the directional landforms tool in Landscape Connectivity and Pattern tools for ArcGIS within a 90m window, we identified flat and open areas, slopes, and steep areas. We also included a covariate for elevation with and without a quadratic term. We classified any pixel with a value <2400m (upper bounds of golden eagle nests) with a change in slope >15 degrees as cliff feature. Pixels in the DEM were classified as a cliff or non-cliff cell based on whether they met the topographic conditions, and the proportion of identified cliff pixels was calculated across all spatial scales.

High quality foraging habitat near nest sites is vital to raising young, and golden eagles typically choose undisturbed sagebrush-steppe habitats with little topographic relief to hunt prey (Phillips et al. 1984, Kochert et al. 2002). We used data that estimated the percent cover of herbaceous vegetation, sagebrush, and shrub coverage, as well as shrub height at 30m resolution (Homer et al. 2012). We calculated the mean and standard deviation of each habitat metric at each spatial scale to estimate landscape heterogeneity, which may be related to higher prey populations. Because golden eagles largely avoid forested habitat while foraging (Kochert et al.

2002), we hypothesized nest sites would have a negative association with proportion of forested areas at large scales. To capture forested habitat, we reclassified LANDFIRE existing vegetation cover as forested and non-forested, classifying forested habitat as all non-riparian treed vegetation types (www.landfire.gov). Anthropogenic features relevant to golden eagle ecology that were spatially available across Wyoming, included roads, tillage agriculture, and oil and gas wells. We hypothesized that golden eagles would avoid agriculture at all scales (Olendorff 1976, Craig and Craig 1984, Phillips et al. 1984, Marzluff et al. 1997, Carrete et al. 2005), and quantified the prevalence of agriculture as the proportion agricultural land within each scale. Data were interpreted from National High Altitude Program (NHAP) color infrared aerial photography or collected with GPS units. Wyoming Water Resources Division provided data on irrigated agricultural lands that we used with a non-irrigated agricultural lands data source, maintained by Wyoming Geographic Information Science Center (WYGISC, http://www.uwyo.edu/wygisc), and a University of Montana irrigated land layer.

Infrastructure associated with oil and gas development is a pervasive feature in Wyoming sage-steppe habitats and includes transmission lines, well pads, roads, and compressor stations. Federal land management agencies require wildlife surveys prior to development. Thus, most survey efforts for golden eagle nests occurred within close proximity of oil and gas developments. Spatial survey bias can have important impacts on model interpretation in habitat suitability studies (Phillips et al. 2009). The intention of selecting a background group of available sites is to provide a sample of the set of conditions available to the species within the area of interest. If the surveys are not representative of the sampled distribution – in our case, most of Wyoming – then there will likely be bias within the data. Temporal predictor variables of nests and wells may address the potential for biased relationships between nest site selection

and well pad density, but sampling of golden eagle nests is still non-random with respect to the energy landscape. In fact, >90% (78% within 3km, 40% within 1km, and 6% within 200m) of nest territories in our dataset are within 5km of an active well underscoring the potential for sampling bias. Thus, we did not include oil and gas well metrics or roads, often associated with energy development, implicitly in our analyses.

We examined if the sampling bias associated with oil and gas development pervaded to covariates in final models by calculating pairwise correlation coefficients between each covariate in predictive models and a metric for oil and gas development among nest sites and available locations. To obtain a measure of oil and gas development, we calculated the number of producing wells prior to nesting dates within each spatial scale around nest sites, using the average date nesting of 23 May for all available sites and nest sites with missing date information. Choosing the best fit scale similar to analyses above, we used the resulting metric for each region for correlation calculations. We determined that covariates used to predict nest-sites would not be biased by the sampling scheme if 1) covariates used in final models and oil and gas measures were weakly correlated ($|r|<0.3$), and 2) correlations among variables at available sites were not systematically larger than those at used sites. All spatial layers were processed in ArcGIS Desktop V.10.1 (http://www.erdas.com) and retained or resampled to 30m raster data.

Model Development

We developed resource selection functions (RSFs) with a use-availability framework to estimate the relative contribution of predictor variables to nest-site selection by golden eagle (Johnson et al. 2006). Our aim was to select the best fit term among related variables in the candidate set to use for multivariate modeling. This included choosing a best fit spatial scale

among variables, determining whether standard deviation added to model parsimony, and deciding if a quadratic term was appropriate. We compared Akaike Information Criteria (AIC) values among models with the same descriptive variable to determine the best fit spatial scale, and compared AIC values of all models to that of a null logistic regression model. Quadratic terms were competed against the same untransformed univariate models. Once the best fit term was selected from each variable, we examined the correlation structure among variables using pairwise Pearson's correlation coefficients among all variables. Highly correlated variables ($|r| \geq 0.60$) were not included in the same multivariate model. When two variables were highly correlated, we selected the variable with the lowest univariate AIC score for use in multivariate models. This resulted in a suite of variables for each region that was included in the model set for RSF models. We used resulting variables to fit regional global multivariate models for map-based predictions.

Model Evaluation

Using a model evaluation technique developed for RSFs with a use-availability design by Boyce et al. (Boyce et al. 2002), we portioned data using k-fold cross validation with five folds for each region. We iteratively fit global models for each set of training folds, and calculated the area-adjusted observed number of observations falling into 10 binned RSF classes. We calculated the Spearman rank correlation between the RSF score and the area-adjusted frequency of validation points for each of the five folds and the mean area adjusted frequency across folds. High correlation values between RSF scores and area-adjusted frequencies suggest a model that is good at predicting the occurrence of golden eagle nests (Johnson et al. 2006).

Forecasting Wind Development Risk

We converted NREL wind power class (WPC) maps from polygon to raster data, resampling to 30m pixels to match GIS layers used in RSF development (http://www.nrel.gov/gis/wind.html). NREL maps provide an estimate of the annual average wind resources at 50m, delineated into 7 wind power classes (1 lowest WPC, 7 highest WPC), so we similarly reclassified regional RSF maps into 7 geometric bins. We combined WPC maps with RSF maps and generated a raster with each pair of RSF and WPC categories for a total of 49 unique cell values. For each region, we calculated the area of each RSF and WPC combination, and tabulated the number of nest sites and commercial wind turbines (as of 2009) within each category.

RESULTS

Removing possible redundant nests with our hierarchical selection algorithm based on nest spacing, observation year, and activity status (active, occupied, and inactive) identified 1,176 nest sites. Of the 1,176 nest sites 483 were located in the Northwest Great Plains region (NWGP) and 693 were in the Wyoming Basin region (WYB; Figure 2.1). The oldest nest site data were from 1974 and 40% of nest sites were from 2000-2010. Saturating each region systematically with available samples while enforcing 3km spacing between all data point resulted in 4,158 available samples in the NWGP, and 11,053 in the NWGP.

All variables considered in the regional models contained at least one term that fit better than a null model. In the NWGP, best-fit scales associated with variables where either the smallest (200m) scale for cliffs and steep landscapes; or the largest possible scale (5km; Table

2.2), with AIC values increasing or decreasing monotonically towards each selected scale (unpublished data). A standard deviation term improved the AIC score for all sagebrush metrics and an inclusion of a one year lagged effect better modeled the influence of sage-grouse leks and precipitation on nest-site selection. Best fit multi-scaled variables in the WYB were similar to NWGP models except for NDVI and sloped areas (Table 2.2).

Each regional suite of variables contained several predictors that were highly correlated ($r>|0.60|$; Table 2.2). Remaining uncorrelated variables shared the direction of selection (positive or negative) across regions used for global models (Table 2.2). Variables used in global models were not correlated ($|r|<0.24$) with the number of producing oil and gas wells within 5km (Table 2.3).

Global models for each region contained 15 covariates representing topographic indices, prey density, land use, climate, and vegetation (Table 2.4; Figure 2.2). We removed an agricultural predictor variable from the NWGP regional model because the coefficient estimate changed significantly in direction and magnitude from the univariate estimate, suggesting variable instability (Hosmer and Lemeshow 2004). Among variables occurring in each regional model, elevation and temperature differed in the direction for which they influenced nest site selection (Table 2.4). Spearman rank correlation values between the area-adjusted frequency of validation points and RSF bin across the five folds ranged from 0.86–0.95 in the NWGP, and 0.72–0.96 in the WYB, while averages from across folds were high in the NWGP (1.0) and WYB (0.952).

Areas identified as moderate risk (orange and yellow colors; Figure 2.3; Table 2.5) made up the greatest portion of the study area when overlaying NREL WPC maps with reclassified golden eagle RSF maps (Figure 2.3; Table 2.5). Cells considered the highest risk (RSF 7 and

WPC 7) represented the smallest area in both regions (Figure 2.3; Table 2.5), containing no observed nests in the NWGP and 5 in the WYB. Across regions the lowest three WPC (1-3) contained 75% of the known nest sites, while the highest 3 WPC contained only 10% of nests (Table 2.5). The number of wind turbines within each WPC increased monotonically in the WYB; in the NWGP, WPC 4 contained the most existing turbines (Table 2.5). The most wind turbines across regions occurred in RSF bins 3-4, with only 2 turbines occurring in the highest or lowest RSF bin (Table 2.5).

DISCUSSION

We modeled breeding habitat selection for a wide-ranging predator across large spatial scales – over twice the land area of Austria. Our models performed well, despite the generalist nature of golden eagles, likely due to the large number of samples and availability of high-quality GIS data across our study areas. Processes influencing nest site selection in golden eagles are dynamic and complex, including land forms, vegetation, and a temporally-variant climate and prey base. Cliff features at local scales were important predictors in both regions. Selection for flat and open areas in the NWGP could appear at odds with selection for cliff; however, the landform metric for flat and open areas was summarized at 90m, in contrast to the 30m resolution of the cliff metric. The apparent disparity between these metrics likely reflects the selection for areas of sharp relief within flat and open areas.

Eagles demonstrated slight preference for less vegetated areas, demonstrated by a negative association with the Normalized Difference Vegetation Index (NDVI) in the NWGP at the largest scale, and negative coefficient estimates for herbaceous cover at large scales in the

WYB. Higher NDVI values and herbaceous cover may result in higher densities of primary consumers including multiple prey species for golden eagle, though they may also obscure visibility of prey. Lower NDVI values could also distinguish sage steppe from grassland habitats, as golden eagles preferentially selected for sagebrush cover in large contiguous tracts at large scales.

Prey abundance and distribution is paramount in explaining space use of predatory species. Though spatial data on prey abundance and distribution is rarely available across landscape scales. Researchers have used models of prey distribution, including coefficients drawn from RSF models, to explain attributes of predator habitat use (Odden et al. 2008, Hebblewhite et al. 2011). However, our research uses direct measures of prey distribution and abundance to estimate the influence on predator habitat selection. Models suggest golden eagles selected nest sites within landscapes containing greater numbers of sage-grouse leks. This preference may likely capture the spatial and temporal correlation between sage-grouse and cottontail rabbits (Fedy and Doherty 2011), a primary prey resource of golden eagles (McGahan 1968, Kochert et al. 2002).

Infrastructure associated with oil and gas development may influence golden eagle nest-site selection; however, the potential sampling bias within energy landscapes rendered these variables inappropriate for nesting models. This bias did not pervade to the covariates we sampled, as the best estimate of oil and gas was only weakly correlated with variables included in regional models. Investigating the impacts of development requires mechanistic studies beyond the scope of our data, and should include measures of habitat use and overall fitness of individuals. Human disturbance may decrease the probability of golden eagles occupying territories (Martin et al. 2009) and many wildlife species in Wyoming including sage-grouse

(Doherty et al. 2008), antelope (Berger 2004), mule deer (Sawyer et al. 2006), and grassland birds (Bayne et al. 2008) alter habitat use in response to oil and gas development. However, the avoidance documented in other wildlife species may not apply to raptors. Indeed, raptors may selectively use anthropogenic features associated with oil and gas development such as power lines and roads for hunting. In fact, ferruginous hawks (*Buteo regalis*) have been documented nesting on drilling equipment in tree-sparse prairies (Neal 2007). Though a lack of avoidance does not necessarily indicate a lack of impact, and it is possible that features selected in a human-modified landscape may have unintended consequences on overall fitness of raptors (Van Horne 1963).

Despite good model performance, the nest data used to develop our models were not collected according to an optimum sampling design when considering the state of Wyoming as a single study site. Most of the data were collected to address localized research and management needs regarding golden eagle nesting ecology. When designing a research study, investigators should carefully consider the optimum sampling design to address the questions of interest prior to data collection (Thompson 2002). Yet design-based studies in ecology are currently rare at large spatial and temporal scales, and investigators often must combine data from multiple sources. Careful consideration of sampling design and species ecology can help ensure valid conclusions are drawn from the data. For example, the first step in designing a research study involves defining a sampling frame and unit. We defined the sampling frame as the known distribution of golden eagles within Wyoming, though identifying the sampling unit required more consideration. We developed a hierarchical approach to parsing available data to define a biologically meaningful sampling unit. Our approach focused on our specific study objectives and incorporated species behavior, sampling time frames, data quality, and the spatial

distribution of records. We recommend the development of similar approaches when working with datasets collated from multiple surveys with varying study objectives.

NREL wind power class (WPC) and RSF map overlays demonstrated 1) Wyoming landscapes are dominated by areas of moderate suitability to nesting golden eagles and wind development, 2) high quality eagle habitat and high WPC values have minimal overlap, 3) nests tend to occur in lower WPC, and 4) existing turbines tend to occur in lower RSF values. It is important to note that potential wind resources are but one factor leading to the likely installation of wind turbines, demonstrated by the non-monotonic relationship between existing turbines and WPC. Various social, political, infrastructure, and environmental factors likely converge in the decision-making process among stakeholders. Yet energy development is ultimately linked to available resources, and NREL maps provide a powerful broad-scale tool with utility in applied research (Kiesecker et al. 2011,Obermeyer et al. 2011, Fargione et al. 2012) for resource managers and industry. Viewed in total, we found that high quality golden eagle nesting habitat and areas of high value for wind energy installations are largely disparate. Yet our models did classify over 700km^2 as containing the highest quality golden eagle nesting habitat (RSF 5-7) in the three highest WPC. These "risky" areas encompassed 98 known golden eagle nest sites and roughly 1/3 (250) of the commercial turbines in the study area.

Our risk maps provide a biological basis for helping to guide the siting of wind development at local and landscape levels. Our predicted maps contain 30m resolution, and thus have the ability to provide guidance for site-level placement of turbines within existing permitted fields, though we do not suggest that models displayed as maps should replace empirical on-site monitoring. In particular, non-breeding habitat-use should be evaluated when making siting decisions. Anecdotal evidence suggests that most eagle turbine strikes occur during spring

breeding months, though mortalities are seasonally ubiquitous (Nygard et al. 2010, Pagel et al. 2013). Identifying winter raptor concentration areas, juvenile (non-breeding) dispersal areas, and understanding migratory pathways, will be important contributions of applied research towards eagle conservation.

CONCLUSIONS

Minimizing golden eagle mortality and displacement is the major goal in research efforts to identify areas of high species use prior to wind development. Currently, most preconstruction risk assessments are based upon site-level monitoring prior to wind turbine placement. Typically, assessments use abundance indices and assume linear relationships with future mortality (i.e., risk scales directly with observed bird counts). However, studies have found that local abundance is often not correlated with mortality at wind farms (deLucas et al. 2008), and that environmental impact assessments based upon bird counts at sites do not share a relationship with recorded mortality following construction (Ferrer et al. 2011). Large scale, spatially explicit, and empirically driven habitat use models such as those presented here may be better predictors of mortality risk for certain species. For example, Carrete et al. (2012) found that models predicting the distribution and aggregation (e.g., breeding colonies and roost sites) of griffon vultures (*Gyps fulvus*) across large extents had a positive and linear relationship with mortalities at wind farms. Indeed, large scale spatially-explicit models near aggregation areas (e.g., nests) far outperformed pre-construction counts for estimating mortality risk (Carrete et al. 2012). Our overlays of wind potential and probability of nest selection have taken this a step further in an attempt to identify high risk areas prior to development. We suggest the

consideration of our models in concert with site-level multi-season data to help inform development concerned with minimizing impacts to golden eagles in Wyoming. The greatest strength of our products to managers lies in the ability to proactively target areas for conservation where the biological value is highest and the energy development risk is minimal. Used in concert with additional species-level habitat maps purveying risk across Wyoming, including sage-grouse, managers in Wyoming have a scientifically-defensible toolbox to help achieve multiple-species conservation at a landscape level.

TABLES

Table 2.1. List and description of spatial variables hypothesized to influence selection of nests by golden eagles. Subscript denotes if multiple scales, quadratic terms, means and standard deviations, or if temporal lag effects of variables were modeled.

Variable	Description
ag_s	Proportion of tillage agriculture
$cliff_s$	Proportion of cliff habitat
fo_s	Proportion of flat and open habitat (Theobald 2007)
st_s	Proportion of steep habitat (Theobald 2007)
sl_s	Proportion of sloped habitat (Theobald 2007)
$ndvi_{s,q}$	Normalized difference vegetation index averaged between 2004 and 2007
$treed_s$	Proportion of deciduous and coniferous (non-riparian) tree habitat
$r13_s$	Proportion of primary road classes
$elev_q$	Digital elevation model of elevation at 30m resolution
$ppt4_{q,t}$	April precipitation
$tmin4_{q,t}$	April mean minimum temperature
$tmax4_{q,t}$	April max minimum temperature
$herb_{ms}$	Estimate of continuous herbaceous cover at 30m resolution
$sage_{ms}$	Estimate of continuous sagebrush cover at 30m resolution
$shrh_{ms}$	Estimate of shrub height averaged at 30m resolution
$shrb_{ms}$	Estimate of continuous cover of all shrubs at 30m resolution
$countsofmales_t$	Count of greater sage-grouse males on leks in 5km moving window
$countsofleks_t$	Number of active greater sage-grouse leks in 5km moving window

s - variable modeled from moving window of scales 200m, 1-, 3-, and 5km.
ms - calculated value at each moving window scale, and mean and standard deviation at each scale.
q - variable modeled with quadratic term.
t – temporally varying covariate modeled with current year, and 1 year lagged effect.

Table 2.2. Best fit univariate term among competing variables in the Northwest Great Plains (NWGP) and Wyoming Basin (WYB), and coefficient estimate. Asterisks denote correlated variables removed from multivariate RSF models.

Variable	NWGP	WYB
ag	5km (-0.28)	200m (-0.41)
cliff	200m (0.25)	200m (0.60)
ndvi	$5km^2$ (-0.59, 0.06)	$1km^2$ (0.01, -0.18)*
treed	5km (-0.72)	5km (-0.16)*
flat/open	200m (0.24)	200m (-0.34)*
sloped	5km (0.16)	1km (0.29)
steep	200m (0.18)*	200m (0.41)*
herb	$5km_{m,sd}$ (-0.11, -0.36)*	$5km_{m,sd}$ (-0.30, -0.13)
sage	$5km_{m,sd}$ (0.23,-0.47)	$5km_{m,sd}$ (0.08, -0.17)
shrh	$5km_{m,sd}$ (-0.15,-0.56)*	$5km_{m,sd}$ (0.08-0.12)*
shrb	$5km_{m,sd}$ (-0.05,-0.17)*	$5km_{m}$ (-0.18)
sg lek count	lag (0.29)	cur (0.14)
sg malecount	lag (0.25)*	lag (-0.06)*
tmin	cur^2 (0.21, -0.19)	cur^2 (0.19, -0.15)
tmax	cur^2 (0.14, -0.10)*	cur^2 (0.16, -0.16)*
ppt	lag^2 (-0.08, -0.15)	cur^2 (-0.10, -0.06)
elev	(-0.49, -0.18)	(-0.06, -0.18)

m – mean; sd-standard deviation; ^{2}-quadratic term;
cur – current year; lag – 1 year lagged
* Correlated variable removed for inclusion in multivariate model

Table 2.3. Pairwise correlation values between variables used in global RSF models and best fit term associated with oil and gas development (producing wells within 5km).

NWGP			WYB		
Variable	Available	Used	Variable	Available	Used
ag 5km	0.14	0.16	ag 200m	0.01	-0.04
cliff 200m	-0.03	0.16	cliff 200m	-0.02	-0.03
ndvi 5km	-0.02	0.08	slope 1km	-0.03	-0.14
ndvi $5km^2$	-0.11	-0.14	herb 5km m	-0.03	-0.05
treed 5km	-0.12	0.00	herb 5km sd	0.00	0.03
flat/open 200m	-0.01	-0.05	sage 5km m	-0.04	-0.21
slope 5km	0.00	0.23	sage 5km sd	0.00	-0.12
sage 5km m	-0.03	0.01	shrb 5km m	-0.04	-0.10
sage 5km sd	-0.02	0.05	lek count	-0.03	-0.08
lek count lag	-0.03	0.02	tmin	-0.05	-0.09
Tmin	-0.07	-0.20	$tmin^2$	0.04	-0.07
$tmin^2$	-0.06	-0.06	ppt	0.02	0.04
ppt lag	0.04	0.14	ppt^2	0.02	-0.05
ppt lag^2	-0.08	-0.12	elev	-0.03	-0.13
Elev	0.00	-0.09	$elev^2$	0.01	0.03
$elev^2$	-0.14	-0.03			

Table 2.4. Coefficient estimates and standard errors for global RSF models in the Northwest Great Plains (NWGP) and the Wyoming Basin (WYB).

NWGP			WYB		
Variable	β	SE	Variable	β	SE
cliff 200m	0.38	0.042	ag 200m	-0.07	0.087
ndvi 5km	-0.53	0.083	cliff 200m	0.64	0.028
ndvi $5km^2$	-0.02	0.072	slope 1km	0.11	0.052
treed 5km	-0.53	0.146	herb 5km m	-0.41	0.079
flat/open 200m	0.38	0.051	herb 5km sd	0.03	0.089
slope 5km	0.29	0.064	sage 5km m	-0.01	0.071
sage 5km m	-0.02	0.065	sage 5km sd	0.00	0.070
sage 5km sd	-0.40	0.066	shrb 5km	-0.20	0.081
lek count lag	0.23	0.045	lek count	0.18	0.030
tmin	-0.07	0.069	tmin	0.11	0.057
$tmin^2$	-0.10	0.049	$tmin^2$	-0.11	0.037
ppt lag	-0.15	0.065	ppt	-0.11	0.057
ppt lag^2	-0.10	0.050	ppt^2	-0.07	0.037
elev	0.75	0.079	elev	0.21	0.086
$elev^2$	0.06	0.055	$elev^2$	0.01	0.052

Table 2.5. Area (km^2) and the known number of nests (in parentheses) found overlapping cells between golden eagle RSF and NREL wind power class (WPC) map in the Northwest Great Plains (NWGP) and the Wyoming Basin (WYB). Values on outside of tables represent the number of wind turbines in each category as of 2009. Cell colors correspond to map in Figure 2.3.

Golden Eagle RSF Bin

NWGP

NREL WPC	1	2	3	4	5	6	7	
1	47.92689 (3)	26.60661 (2)	23.50647 (3)	37.60155 (5)	42.08544 (3)	30.44529 (5)	24.33618 (18)	0
2	107.86221 (4)	77.74047 (9)	96.05232 (11)	179.69058 (7)	287.08326 (16)	429.26958 (48)	327.21642 (81)	0
3	64.59921 (1)	128.79882 (12)	140.19246 (10)	252.54153 (8)	415.98378 (21)	540.94797 (40)	452.29752 (80)	16
4	52.84116 (1)	120.04587 (10)	119.64897 (8)	173.57472 (5)	223.2342 (20)	204.74253 (17)	67.4262 (16)	126
5	38.11329 (1)	27.95319 (2)	23.87817 (3)	57.80313 (1)	66.93408 (6)	19.12518 (3)	2.01438 (1)	40
6	14.98482 (0)	3.84813 (0)	5.58297 (1)	16.33347 (0)	5.39865 (0)	0.73674 (1)	0.25272 (0)	53
7	1.54008 (0)	0.01044 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
	11	45	91	59	28	1	0	

WYB

NREL WPC	1	2	3	4	5	6	7	
1	615.86109 (8)	763.2495 (23)	550.68138 (19)	575.93511 (12)	350.01909 (11)	169.42464 (14)	124.98093 (40)	0
2	253.49283 (5)	337.77009 (11)	335.9655 (2)	635.91903 (19)	1083.3786 (43)	430.92216 (32)	145.30068 (62)	0
3	102.31407 (4)	140.96943 (5)	214.94943 (9)	449.54514 (12)	1306.27449 (43)	700.58574 (59)	127.27476 (66)	46
4	35.24544 (0)	54.35991 (2)	100.50408 (4)	213.0111 (10)	480.43476 (16)	315.11646 (21)	79.29846 (34)	87
5	16.2108 (0)	34.23312 (2)	45.13932 (5)	98.92755 (6)	197.76249 (12)	141.44553 (10)	40.72932 (24)	101
6	18.35973 (0)	31.48092 (2)	42.35697 (1)	61.1505 (4)	99.36531 (3)	97.83972 (12)	27.93402 (19)	115
7	4.54104 (0)	10.09962 (0)	10.51803 (0)	10.57203 (0)	13.48263 (0)	18.56817 (2)	7.56621 (5)	141
	0	55	145	117	75	96	2	

FIGURES

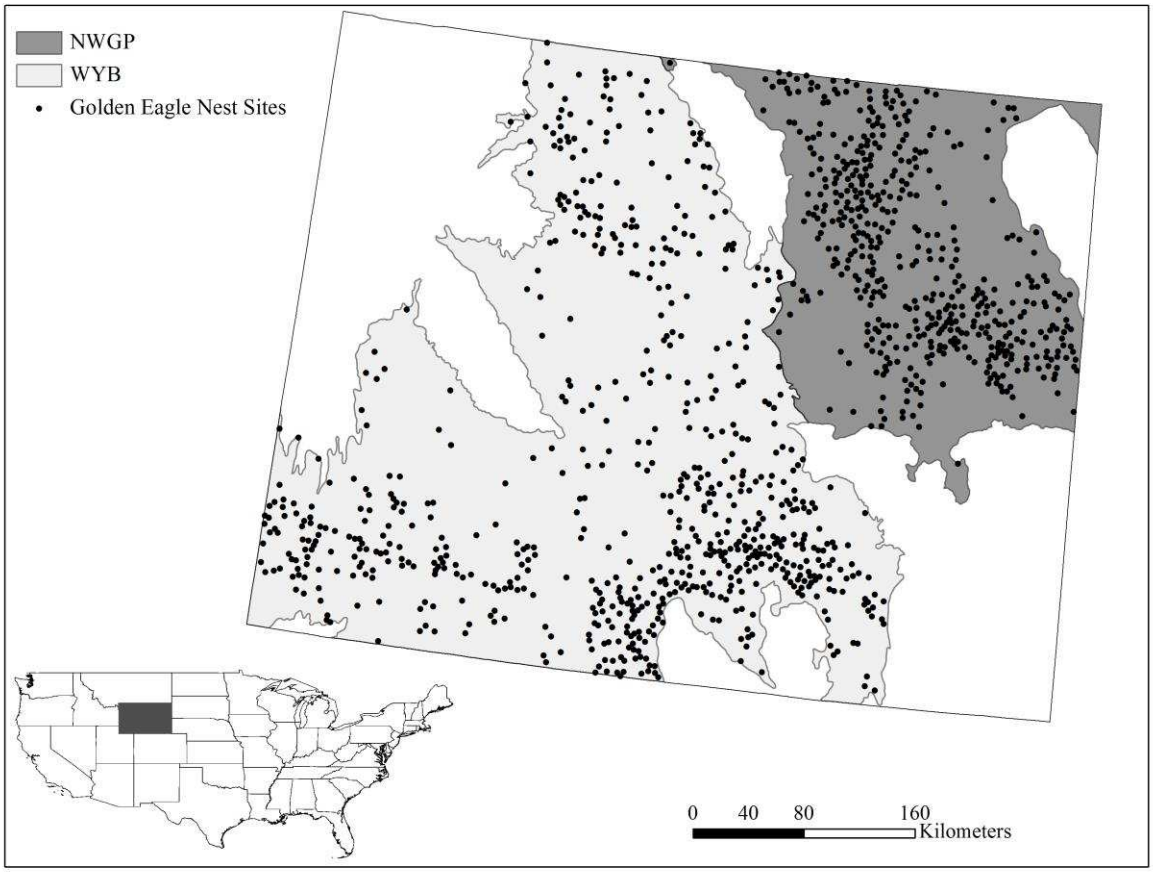

Figure 2.1. North *American* Commission of Environmental Cooperation (NACEC) level II ecoregions Northwest Great Plains (NWGP; dark gray), and Wyoming Basin (WYB; light gray) portions of Wyoming, USA. Reducing nest site data to remove redundant and clustered data produced 1,176 total nest sites, 483 in the NWGP and 693 in the WYB.

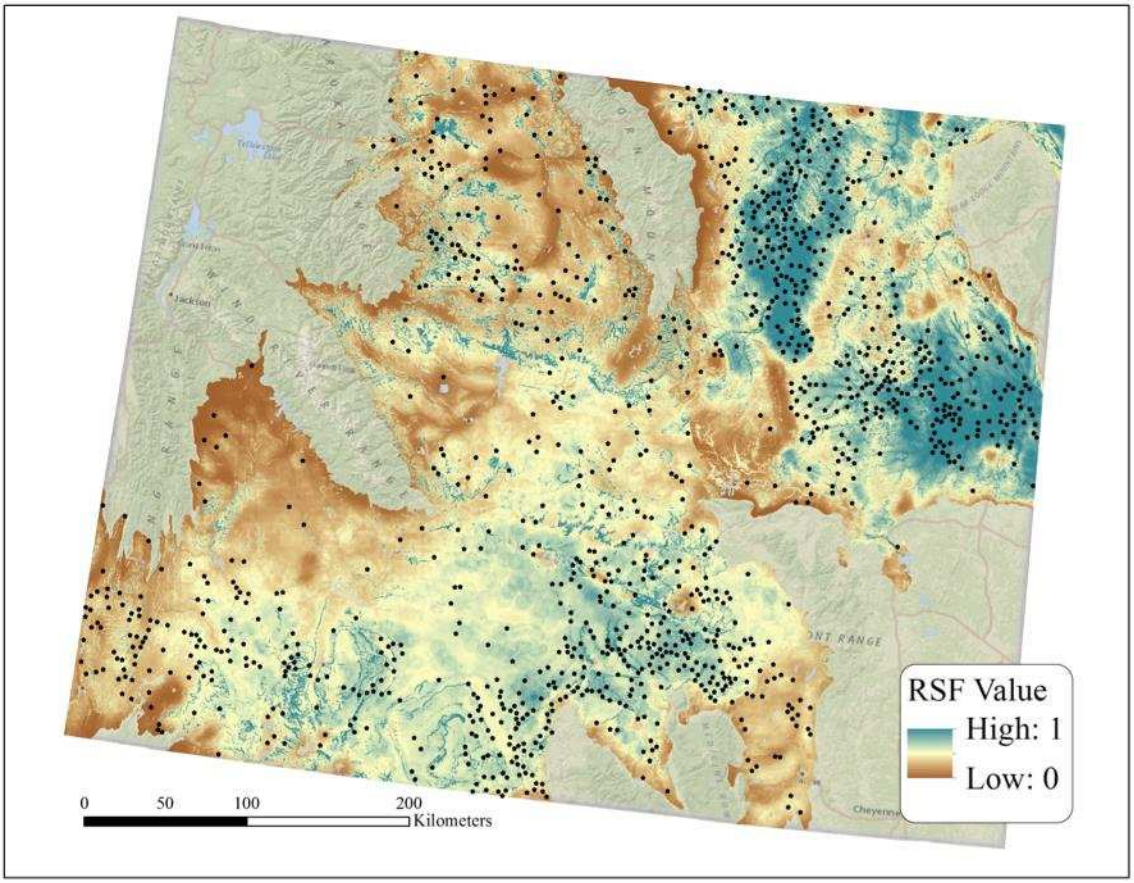

Figure 2.2. Resource selection function (RSF) probability grids across the Northwest Great Plains (NWGP) and Wyoming Basin (WYB) regions in Wyoming, USA. RSF values represent the probability proportion to use of golden eagle nest site. Predictions are based on a global model for each region.

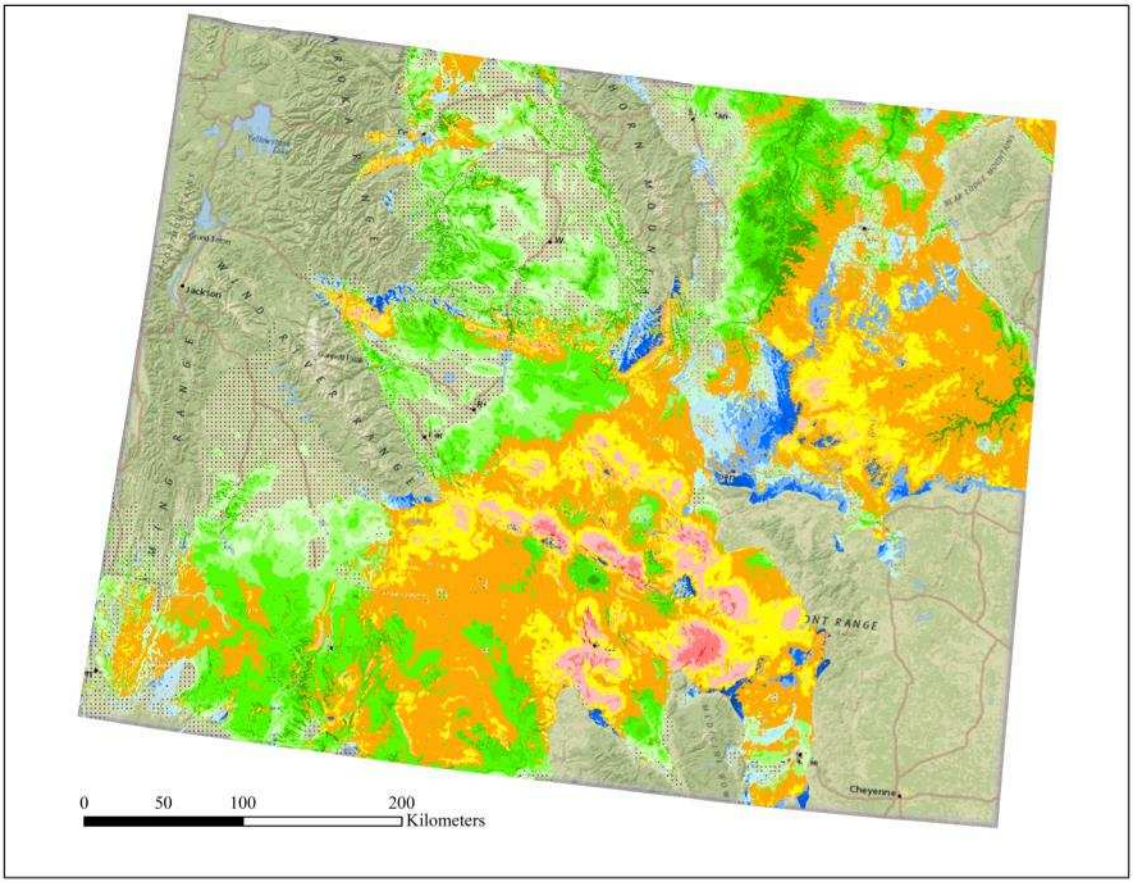

Figure 2.3. Spatial delineation of overlay between seven NREL wind power classes (WPC; 1-low wind value, 7-high wind value) and regional resource selection function maps grouped into seven geometric bins (see Table 2.5 for color legend). Hatched areas are predicted low value for golden eagle nesting and wind development.

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Chapter 3: Ecosystem processes and an anthropogenic footprint converge to shape dynamic distributions of a wide-ranging predator.

INTRODUCTION

Investigating the relationships between a species and its environment has been a fundamental pursuit of ecologists over the past century leading to understanding of ecosystem complexity and species distributions (Grinnell 1917). From a conservation perspective, there is an underlying urgency to identify and understand the relationships between a species and its habitat in light of unprecedented global change in both land use and climate (Steffen et al. 2007). Current and projected losses of species habitat from anthropogenic impacts are staggering, and influenced from multiple sources including energy development (Allred et al. 2015) and agriculture (Tilman et al. 2001). The concerns with direct habitat loss and transformation are often exacerbated by human-caused climate change and expanding distributions of exotic species (Walther et al. 2002). Thus, identifying landscapes with the necessary attributes for successful conservation of species of concern is a pressing challenge for contemporary researchers. It is prescient then, that the conservation community has responded to the challenge of conserving biodiversity with an increasingly biogeographic approach (Whittaker et al. 2005). These efforts have lead to the rapid development and use of analytical tools to produce spatially-explicit estimates of distributions, colloquially termed species distribution models (SDMs; Guisan et al. 2013).

Generally, SDMs are a vehicle for understanding complex ecological relationships by relating a suite of environmental covariates to species locations using either statistical models or

machine-learning algorithms. Common applications within a conservation context include reserve-design and guiding intervention efforts (e.g. translocation, or exotic species-removal). In practice, SDMs are overwhelmingly static, providing a snapshot of the species-environment relationship over some temporally bound window. Implicitly, these static models assume the relationship between a species and its environment is at equilibrium, and projections portend that relationships remain consistent through time (niche conservatism). Yet in light of ongoing global change, occupancy-environment relationships that shape species distributions may be dominated by transient dynamics in response to changing landscapes (Yackulic et al. 2015). For species with populations that are limited by bottom-up forces of diverse and dynamic food resources, such as wide-ranging predators, it is essential to explicitly account for the dynamic nature of distributions (Nielsen et al. 2010).

Golden eagles (*Aquila chrysaetoes*) are an iconic raptor of vast, rugged landscapes across the northern hemisphere, with annual ranges that can be continental in scale (Kochert et al. 2002). In the western United States (US), golden eagle populations are at best considered stable (Millsap et al. 2013, Nielson et al. 2014), though there is a growing concern that increased anthropogenic development will threaten these long-lived predators. In particular, the US is one of many nations expected to experience increased growth in renewable energy development, of which wind energy will play a prominent role (EIA 2013). Wind turbines are a known source of mortality for golden eagles (Hunt 2002, Pagel et al. 2013), which is troubling given even small perturbations to adult survival can result in population-level declines (Whitfield et al. 2004, Chevallier et al. 2015). Energy production from wind turbines may increase by an order of magnitude over the next 35 years in the US (EIA 2013), adding urgency to guide development in areas expected to have the least impact on wildlife populations.

SDMs can be useful tools for prioritizing conservation efforts for golden eagles with an eye towards future wind development (Tack and Fedy 2015), particularly within a regulatory framework that behooves industry to avoid litigation by identifying wind energy projects in areas posing the lowest potential harm to populations (http://www.fws.gov/windenergy/eagle_guidance). However, static models may belie the dynamic nature of golden eagle space use, particularly during non-breeding seasons when individuals are no longer tied to nest sites and expand their home ranges (Watson et al. 2014). Models that estimate parameters to account for the dynamic nature of species distributions have recently been developed and proven useful in SDMs (Guisan and Zimmermann 2000, Guisan and Thuiller 2005). Dynamic occupancy models in particular provide a modeling framework for estimating transitions in site-occupancy via colonization and persistence processes, while accounting for a heterogeneous observation process (MacKenzie 2006) and spatial dependency inherent in species location data (Yackulic et al. 2012, Bled et al. 2013).

We quantified dynamic occupancy patterns for golden eagles during the non-breeding late summer season using data from a US west-wide annual survey (Nielsen et al. 2010). Our objectives were threefold: 1) to parameterize a model that accounts for the dynamic use of habitat over time, while accounting for imperfect detection and spatially-correlated responses in the data; 2) elucidate the ecological processes of how climate, ecosystem processes, and human settlement patterns converge to shape distributions; and 3) develop predictive models that aid in conservation planning with respect to golden eagles and future wind development. We developed a Bayesian hierarchical model that estimated the relationships among environmental variables and golden eagle use across a large spatial extent. Additionally, we described the

dynamic nature and temporal variability of space use by a wide-ranging predator while explicitly accounting for an imperfect observation process and spatial confounding of parameter estimates.

METHODS

Study Area and Golden Eagle Surveys

Golden eagles were surveyed from 2006-2012 using fixed-wing aircrafts across four US Bird Conservation Regions (BCRs; 9, 10, 16, and 17; Figure 3.1), spanning the majority of the western US golden eagle distribution. BCRs were developed to encompass ecologically similar attributes, which share common taxa and management issues (http://www.nabci-us.org). Sampled regions encompass shrublands and desert of the Great Basin (BCR 9), prairies and badlands of the western Great Plains (BCR 17), and mixed vegetative communities including forested landscapes in the intermountain West along the Rocky Mountains (BCRs 10,16). Natural landscapes are fragmented by tillage agriculture, urban areas, and infrastructure associated with human development including energy development. Surveys occurred each year over a four-week period during late summer (18 August to 9 September). During this time, juvenile eagles have fledged and dispersed from nesting territories, and are no-longer dependent on parental care.

Two survey teams were each composed of three observers (with few flights containing two observers in 2008) and one pilot who flew 100km transects at 150m above ground level (AGL) in relatively flat habitat, while flying lower at 100m AGL in more rugged landscapes. Front and rear observers on the right side of the aircraft independently searched for perched or flying golden eagles, while the third, rear-seated side observer searched for golden eagles to the

left side of the plane. A partition between the front and rear seat ensured observer independence, and because right-side observers did not communicate detections until they passed an eagle, their efforts were viewed as two independent surveys of the same area. Observers recorded the location, age class (subadult or adult), count, and behavior (perched, flying) for all eagle detections. Not all transects could be surveyed each year due to wildfire or other access issues. In these cases, alternate transects were chosen and surveyed. We only used data from transects surveyed at least twice over the duration of the study to assess changes in occupancy over time. For more detail on the survey methodology and design, see Good et. al (2007).

We sought to explain variation in eagle distributions at an ecologically-relevant spatial scale, which required dividing each 100km transect into multiple sites. Thus, we generated sample sites that were roughly the size of a golden eagle territory during the late summer (Marzluff 1997), by subsetting each transect into 20 sites that were 10km segments along each side of flight paths extending 1km from a transect. Eagle detections were then assigned to sites based on GPS locations.

Predictor Variables

Golden eagle distributions are shaped by environmental forces and patterns of anthropogenic disturbance, which are both heterogeneous across space and time. Fluctuating resources and a growing human footprint may be particularly relevant to wide-ranging predators, which navigate across large landscapes to track seasonally dynamic prey resources. We identified three classes of covariates we hypothesized would shape eagle use including i) climatological factors and ecosystem processes presumed to underlie prey distribution and abundance, ii) topographic features conducive to foraging and traveling by raptors (Katzner et al. 2012), and iii) a human footprint composed of development and settlement patterns.

During the late summer, golden eagles depend on small to medium-sized primary consumers for prey, primarily lagomorphs (Kochert et al. 2002). Data on prey distribution or abundance do not exist across the spatial of temporal extent of our study. However, we assumed that primary productivity, and drought severity would be indicative of prey distribution and abundance at large spatial scales (Huntly and Inouye 1988). We extracted remotely sensed gross primary productivity (GPP) data available at 1km resolution over 8 day intervals (http://modis.gsfc.nasa.gov/data), attributing the most recent derived GPP index to flight surveys. Similarly, we hypothesized that drought conditions at local scales would depress herbivore populations (Myers and Parker 1975). We represented our drought hypothesis with a covariate using available Standardised Precipitation-Evapotranspiration Index (SPEI) data (http://sac.csic.es/spei/database.html), a multiscalar drought index summarized over 3 (summer drought; June 1 - September 1) and 12 month (annual; September 1 – September 1) periods.

We calculated a terrain ruggedness index (TRI; Riley et al 1999) using 30m elevation data from the National Elevation Dataset. Among sample sites, we calculated the mean and standard deviation of TRI cells to capture heterogeneity in ruggedness within sample sites.

Independently exploring components of anthropogenic disturbance would greatly increase the parameter space of already complex models, and we were more broadly interested in the human footprint as a whole. Thus, we extend methods developed by Kiesecker *et al.* (2011) to combine multiple sources of temporally dynamic information on energy development, cultivated agriculture, urban development, and road networks into a comprehensive layer to characterize non-natural landscapes. To characterize croplands, we extracted areas identified as cultivated cropland types using available National Land Cover Datasets (NLCD) from 2006 and 2011. We also identified cells characterized as low to high-intensity urban areas from NLCD

data to capture human settlement. Road surfaces, and other human development features were characterized using NLCD Impervious surface layers.

We obtained well location, status, and drilling (spud) date from state oil and gas commissions. If a producing well was drilled prior to surveys, we converted point data to a binary raster (well or no well) for each year. We applied a similar process to location data available for wind turbines (Diffendorfer et al. 2014). Lastly, we used a USGS Topographic Change Polygon, which delineates mines and other areas of human impact that result in non-natural changes in elevation (http://topochange.cr.usgs.gov; accessed March 2013). Each spatial data set was summarized in a binary response of disturbed or undisturbed using the resolution of the largest the minimum mapping unit (30m). NLCD data was the only information that was not available for each year of the study, so we applied values using data from previous years (2006 and 2011) to calculate covariates.

Model Fitting Algorithm

We fit a Bayesian hierarchical parameterization of a dynamic occupancy model (Royle and Kery 2007) to golden eagle survey data. Using the framework, an observation of at least one eagle in a given year (t) at a site (i) by one of two replicate observers (j), arises from joint probability of the latent state of a site truly being occupied $(z_{i,t})$, and the probability that an eagle is detected by at least one of the observers $(p_{i,j,t})$ over the course of $J_{i,j,t}$ surveys.

$$y_{i,j,t} \begin{cases} 0 & ; \text{ when } z_{i,t} = 0 \\ \text{Binomial}(J_{i,j,t}, p_{i,j,t}); & \text{ when } z_{i,t} = 1 \end{cases}$$

True site occupancy, or 'use' by eagles is estimated from a Bernoulli distribution following the probability of occurrence $(\psi_{i,t})$ in the first year.

$$z_{i,2006} \sim \text{Bernoulli}(\psi_{i,2006})$$

In subsequent years (2007-2012), we modeled the demographic processes associated with dynamics of site use including persistence $(\phi_{i,t})$ - the probability that at site is used in successive years, and colonization $(\gamma_{i,t})$ - the probability that an unused site in year *t* is subsequently used in year *t+1*, which we use to interpret as shifts in distributional patterns (Bled et al. 2013). Transition probabilities of persistence and colonization are autoregressive in nature, conditional on occurrence in the previous year.

$$z_{i,t} \begin{cases} \text{Bernoulli}(\phi_{i,t}) \text{ ; when } z_{i,t-1} = 1 \\ \text{Bernoulli}(\gamma_{i,t}) \text{ ; when } z_{i,t-1} = 0 \end{cases}$$

Occurrence probability following the first year of observation is then derived from a previous state, along with site-specific transition probabilities.

$$\psi_{i,t} = \psi_{i,t-1}\phi_{i,t} + (1 - \psi_{i,t-1})\gamma_{i,t}$$

We were primarily interested how multiple factors influence heterogeneity in site use by golden eagles, and built logit-linear covariate models to explain variation in the processes of detection, initial occurrence, and site dynamics (persistence and colonization). We considered coefficients for initial occupancy, persistence, and colonization parameters including covariates for human footprint $(dist)$, gross primary productivity (gpp) including a quadratic term, drought severity indices $(spei3, spei12)$, and terrain ruggedness using the mean $(tri.m)$ and standard deviation $(tri.sd)$ of indices. We also calculated a covariate for site length $(site)$, as not all subsections at the terminal end of transect resulted in exactly 10km sites, though we only included sites that were at least 5km in length.

We deemed it necessary to account for potential lack of independence among sites within each transect because we subset original sample units (transects) into smaller sites. Thus, we calculated a variable that measured the estimated transect density $(D_{i,t})$ for each flight transect

(n_k), based on the number of estimated occupied neighbors divided by the size of the neighborhood (l_i).

$$D_{i,t} = \frac{1}{l_i}\sum_{l \epsilon n_k} z_{i,t}$$

We included this autologistic covariate to explicitly account for spatial dependency among occupied states in parameters for initial occupancy, colonization, and persistence (Hoeting et al. 2000).

Because we suspected that the same processes would explain variation among all occupancy parameters, covariate models used to estimate parameters describing initial occupancy and subsequent dynamics all shared a similar formulation with separate parameter estimates.

$$\psi_{i,2006} = logit^{-1}(\alpha_0 + \boldsymbol{\alpha}'\boldsymbol{X}_{i,2006})$$

$$\phi_{i,t} = logit^{-1}(\beta_0 + \boldsymbol{\beta}'\boldsymbol{X}_{i,t})$$

$$\gamma_{i,t} = logit^{-1}(\delta_0 + \boldsymbol{\delta}'\boldsymbol{X}_{i,t})$$

We considered models for detection probability by including covariates for transect length, as some sites near the terminal ends of surveys were <10km. Front observers had increased visibility and therefore, we also included a surveyor-specific covariate coded to identify surveys by front and rear observer's (obs) as we suspected that front observers would benefit from a better view (Ryan Nielsen, WEST Inc., Personal Communication).

$$p_{i,j,t} = logit^{-1}(\rho_0 + \rho_1{}^* obs_{i,j,t} + \rho_2{}^* site_{i,t})$$

All measured covariates were scaled, mean centered and divided by the standard deviation, for convergence. For each estimated parameter ($\boldsymbol{\alpha}, \boldsymbol{\beta}, \boldsymbol{\delta}, \boldsymbol{\rho}$) we used vague normal prior distributions ($\mu = 0,\ \sigma^2 = 1000$), as there was limited information on golden eagle space

use at the spatial and temporal scale of our study. We estimated posterior distributions from 2 MCMC chains using 10,000 iterations following 20,000 sampled as burn-in. We visually inspected chains and calculated Gelman-Rubin convergence diagnostics across parameters to confirm parameter estimates had converged (Gelman and Rubin 1992).

Model Selection

We did not include highly collinear covariates ($r > |0.6|$) in the model. Furthermore, we first fit models without an autologistic covariate (e.g. non-spatial models) in a likelihood framework with R package unmarked (Fiske and Chandler 2011) and used AIC model selection to determine the best non-spatial structure of covariate models (Burnham and Anderson 2002, Broms et al. 2014). We chose a model structure by first finding the most parsimonious covariate structure for detection probability, with all measured covariates used on occupancy parameters. We then fit all possible combinations among non-correlated covariates among occupancy parameters, selecting the model with the lowest AIC score to consider in Bayesian models with an autologistic term. Across using all possible combinations we used a time-invariant intercept term for persistence and colonization parameters to reduce the number of models run. Once we identified the covariate model structure, we fit one additional model with time-varying intercepts, again using AIC to determine the structure for predictive models.

RESULTS

In total we classified 3540 sites across 220 transects. From 2006-2012, there were a total of 1280 detections of 811 golden eagles across sites. The majority of sites with detections (80.9%) contained only one detected golden eagle, though as many as four eagles were detected

on some sites (0.5%). For a full description of the dataset, readers are referred to Nielson *et al.*, (Nielson et al. 2012).

AIC model selection results for maximum-likelihood models without spatial covariates included coefficients for GPP without a quadratic term, annual drought (SPEI12), terrain ruggedness (TRI), and human disturbance (dist) on covariate models for initial occupancy, and colonization and persistence, in the most parsimonious model. Site length and observer position (front or rear) were both included in the top covariate model for detection probability. Fitting an additional autologistic covariate for transect density to each occupancy parameter using a Bayesian model did not change the direction or magnitude of estimated coefficients. Visual inspection confirmed that posterior distributions had converged, and Gelman-Rubin statistics supported adequate mixing of multiple chains ($\mathbf{r} < 1.01$)

Detection probability was positively influenced by site length ($\rho_2 = 0.069$, 90% CI -0.036-0.170), and observers situated in the front of the aircraft were more likely to detect golden eagles than rear observers (Figure 3.2). Overall probability of detection on given a site ranged from as low as 0.68 (0.59-0.76 90% CRI; for a rear-seated observer on 5km site), to as high as 0.96 (0.95-0.97 90% CRI; 2 observers along a 10km site).

An estimate of initial occupancy (ψ_1) with covariates held at their mean values was 0.027 (0.023-0.032 90% CRI), while colonization (γ) 0.025 (0.024-0.027) and persistence 0.053 (0.040-0.070) were similarly low. Overall trends in occupancy were stable, given time-invariant intercepts for colonization and persistence ($\psi_{2007-2012}$ = 0.024; 0.027-0.028 90% CRI), while turnover rates where relatively high 0.721 (0.719-0.724 90% CRI) across sites. Coefficient estimates for neighborhood density via an autologistic covariate were positive for persistence (β_D= 3.27; 2.69-3.84) and colonization parameters (δ_D=2.84; 1.75-3.87 90% CRI). GPP, TRI,

and human disturbance had consistently negative coefficient estimates across occupancy parameters, while the direction of estimates was equivocal for drought indices. Coefficients estimates were both positive for geographic coordinate covariates (Figure 3.3). Applying posterior mean coefficient estimates to spatial covariate data produced spatially explicit predictions for initial occupancy, colonization, and persistence (Figures 3.4-3.7).

DISCUSSION

The number of wind turbines is projected to grow exponentially in the US (EIA 2013), evolving from a once novel to seemingly ubiquitous anthropogenic feature across wind-swept landscapes. The anticipated growth in renewable energy sources will play an important role in reducing hydrocarbon emissions globally, but may disproportionately impact wildlife habitats as per unit energy wind energy development requires a larger footprint than most other energy sources (McDonald et al. 2009). Therefore, there is a pressing need to identify species-environment relationships that support conservation efforts in light of anticipated development (Tack and Fedy 2015). Yet habitat-use, particularly by wide-ranging predators, is a behavioral trait that is likely not a static through time (Nielsen et al. 2010, Northrup et al. 2015). The dynamic use of space by golden eagles in our study system was characterized by factors that are transient through space and time, including climatic factors (GPP and drought severity), as well as more permanent landscape features including topography and human disturbance. These results are the first large-scale assessment of forces shaping golden eagle distributions outside of the breeding season, using a methodology that is transferable to other species and systems using temporally-replicated detection data.

We found that golden eagles tended not to use areas degraded by a human footprint, demonstrated by negative coefficient estimates for initial occupancy and colonization. However, the impact of human infrastructure on persistent site use was less clear. It's important to note that not all human disturbances may be at odds with habitat use by eagles, and certain infrastructure (e.g. power poles) may actually increase use by eagles (Lehman et al. 2007). For example, Hethcoat & Chalfoun (Hethcoat and Chalfoun 2015) found that decreased nest survival of native passerines was explained by local augmentation of predators that accompanied intensive natural gas development. In fact, areas surrounding Altamont Wind Power Resource Area, a landscape dominated by wind energy infrastructure, is home to some of the highest densities of golden eagles globally, likely due to the high density of California ground squirrels in the area (Hunt and Hunt 2006). Thus it is possible that highly altered landscapes, which happen to support high prey densities may result in consistent golden eagle use.

Unfortunately we were unable to capture prey density with available spatial data across this large spatial scale, and relied on surrogates – GPP and drought severity – in lieu of direct biotic measurements. We found that GPP had the largest effect on occurrence parameters among scaled predictors. GPP as calculated by MODIS measures the amount of photosynthetically useful solar radiation that is absorbed by vegetation, which is then scaled by local vegetation type and climatic conditions. We had hypothesized that larger GPP values would result in concomitantly large prey densities, and thus greater probabilities of eagle use. However, our findings of largely negative coefficients for GPP across dynamic occupancy parameters challenged this hypothesis. Notably, in the Great Basin and shortgrass prairies of North America, grazers are considered resource-limited – such that their population dynamics are driven by bottom-up forces from plant resources (Oksanen 1990). These unique landscapes

represent a challenge to the 'green-world' hypothesis, as vegetation has evolved to sustain the strong pressure by grazers (Hairston et al. 1960). Thus, lower GPP values in our system may be the result of increased herbivory (e.g. high density) by consumers, which include golden eagle prey. Furthermore, low plant biomass may also be conducive to the open foraging grounds preferred by eagles (Kochert et al. 1999).

Golden eagle intraspecific behavior is dominated by territoriality during the breeding season (Watson 2010). However, autologistic coefficient estimates for neighborhood density were high and positive among occupancy parameters, suggesting that these birds of a feather may indeed 'flock' together during the late summer season. While conspecific attraction may explain this finding, we find this explanation unsatisfying for an apex predator. Rather, we suggest that the autologistic coefficient may be subsuming variation in golden eagle space-use unexplained by covariates in the model. Again, lacking accurate spatial prey data may be underlying this finding. Regardless, the magnitude of these coefficients underscores the importance of modeling the spatial structure of the response (e.g. site-occupancy) in our system. Increasingly, SDMs are accounting for spatial dependency using auto-logistic and –regressive terms (Hoeting et al. 2000, Yackulic et al. 2012, Bled et al. 2013), or restricted spatial regression coefficients (Johnson et al. 2013, Broms et al. 2014). This trend is encouraging given that failing to account for spatial autocorrelation in SDMs can result in misleading inference (Dormann 2007).

As practitioners seek conservation planning strategies for golden eagles, the role of space is paramount. In particular, siting (e.g. placement) of wind energy developments and identifying areas for compensatory mitigation (via retrofitting power poles) are two principal management paradigms currently within a regulatory framework for golden eagle conservation (USFWS

2013). Identifying the relationships between golden eagles and their environment can provide support to managers charged with such decisions. Yet we found that site use in our system was characterized by high turnover rates, with variation explained largely by temporally dynamic covariates. Thus a time-invariant snapshot of eagle use may not faithfully represent habitat use for this highly mobile species. This finding may be discouraging to practitioners as 1) managing for spatially invariant processes greatly expands the area necessary for successful conservation and 2) site-level monitoring commonly used for energy siting should span > 1 year. However, our findings support a wind energy development strategy proposed by Kiesecker *et al.* (Kiesecker et al. 2011), which identifies the highly-disturbed landscapes that are likely economically viable for wind development. Our findings also support that these highly disturbed areas may be deemed suitable for development for golden eagles with less monitoring, given that new site-use (colonization) is unlikely.

FIGURES

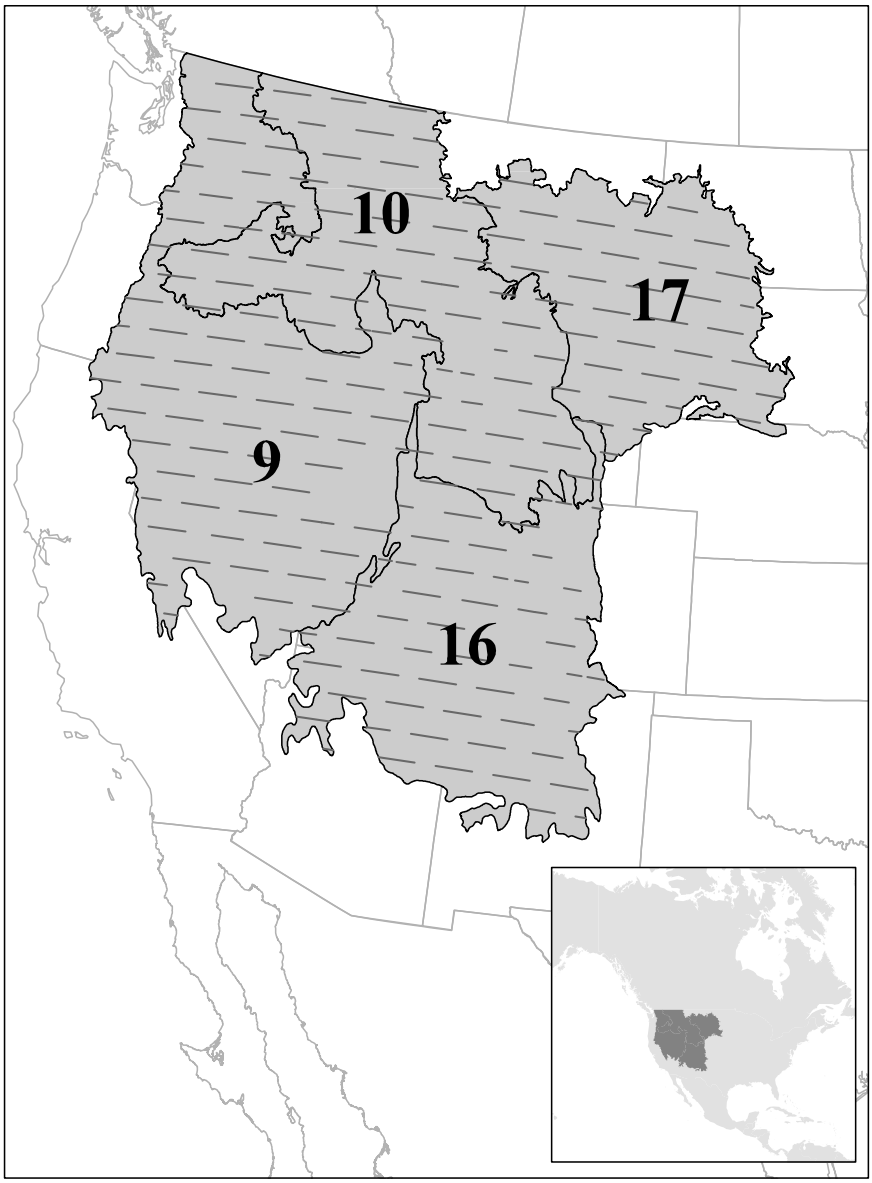

Figure 3.1. Study area encompasses four US portions of North American Bird Conservation Regions: 9 Great Basin, 10 Northern Rockies, 16 Southern Rockies/Colorado Plateau, 17 Badlands and Prairies. Lines represent primary (not alternate) transects from which golden eagles were surveyed by aircraft from 2006-2012.

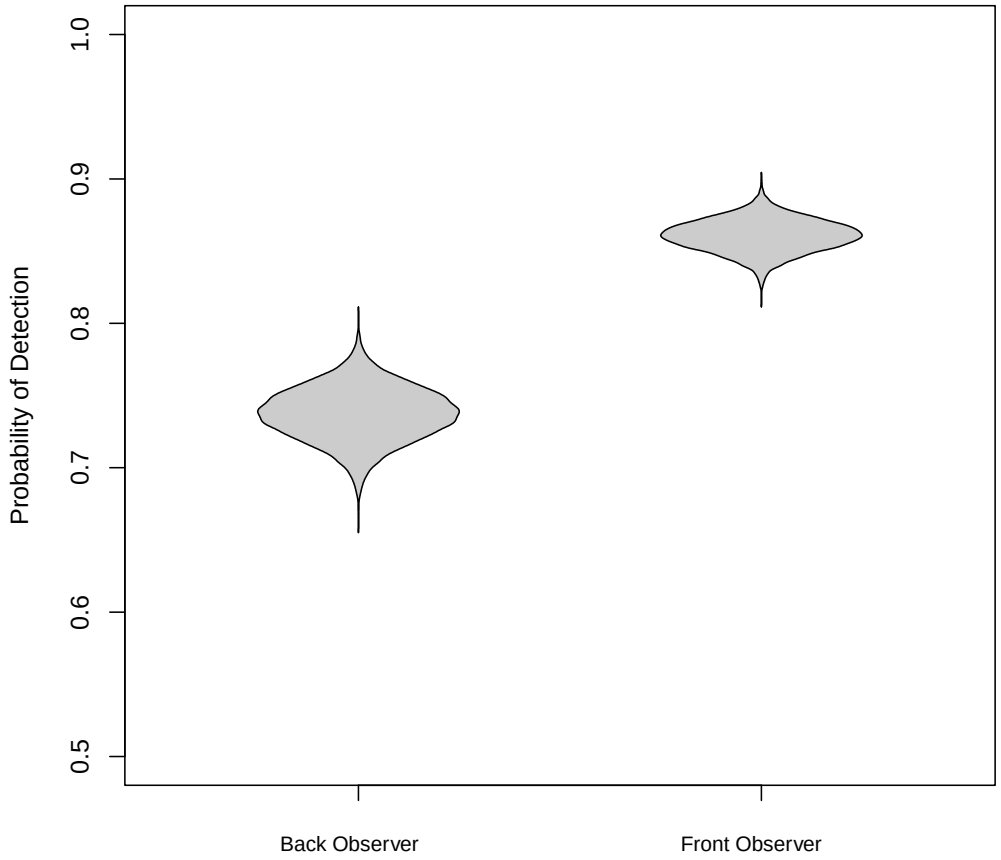

Figure 3.2. Detection probability densities for observers situated in the back (left) or front (right) of the aircraft during aerial surveys, assuming a 10km site.

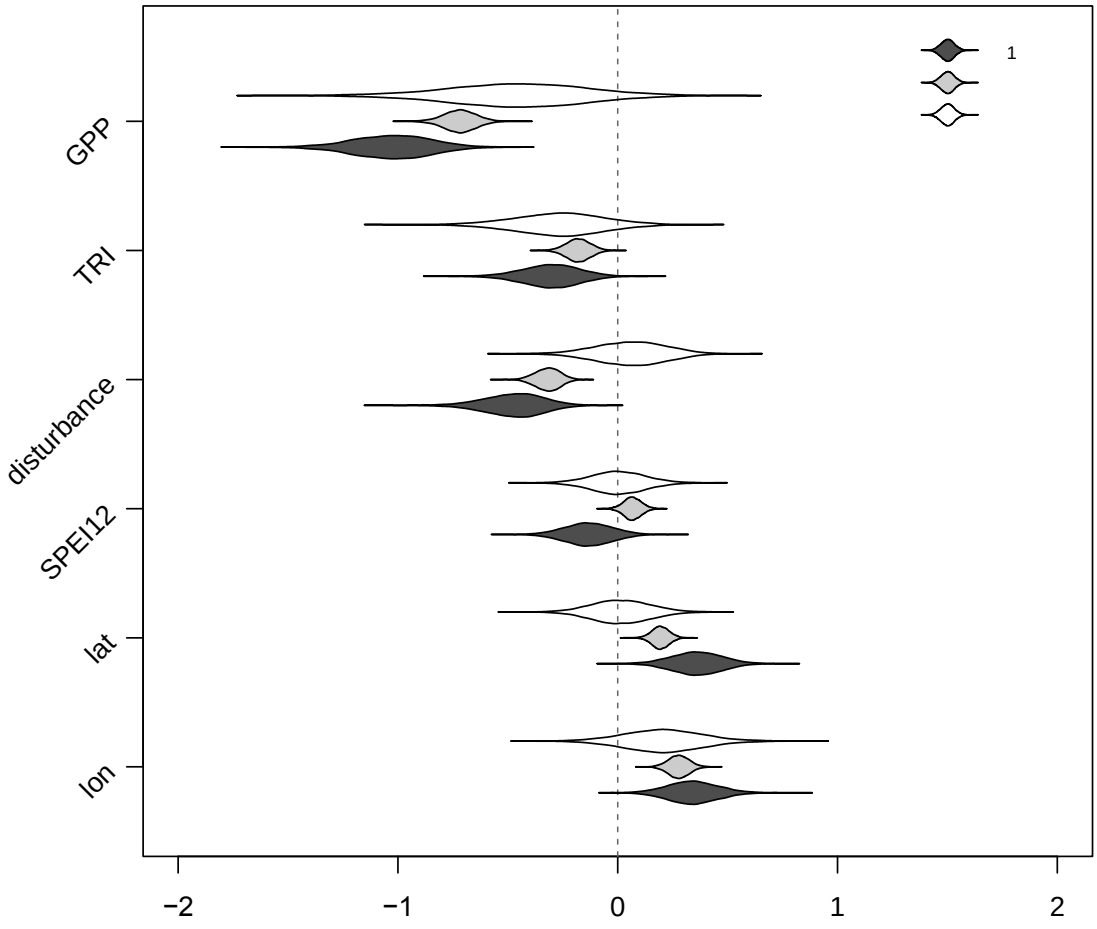

Figure 3.3. Coefficient estimates for gross primary productivity (GPP), Standerised Precipitation Evapotranspiration Indices over a 12-month period (SPEI12), terrain ruggedness (TRI), geographic location (lat and lon), and human disturbance measures (disturbance). Similar parameterizations of covariate models were fit for initial occupancy ($\boldsymbol{\psi_1}$), colonization ($\boldsymbol{\gamma}$), and persistence ($\boldsymbol{\phi}$) probabilities.

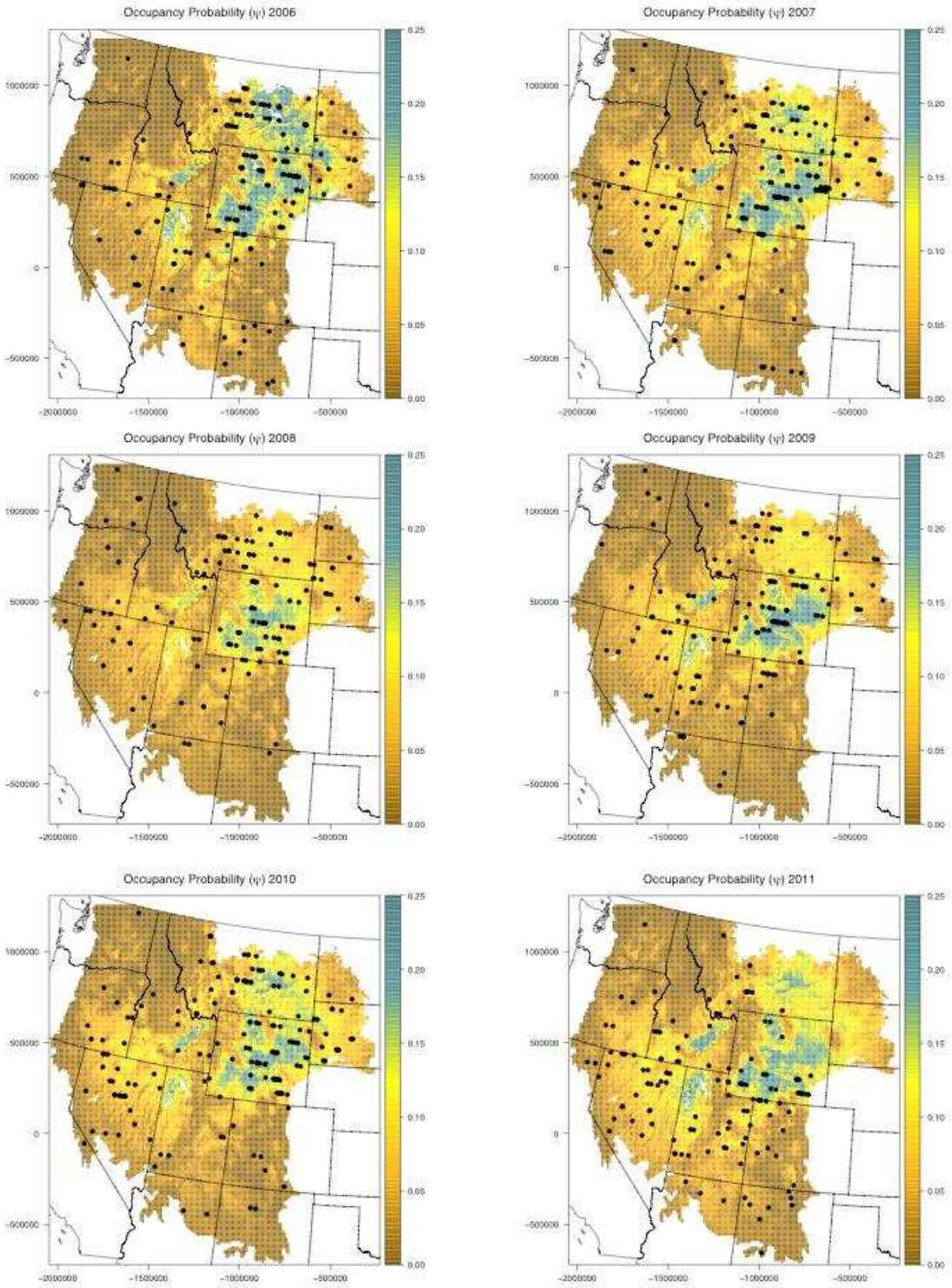

Figure 3.4. Spatial predictions of site occupancy ($\boldsymbol{\psi_{i,t}}$) over time using mean posterior coefficient estimates. Points represent eagle detections.

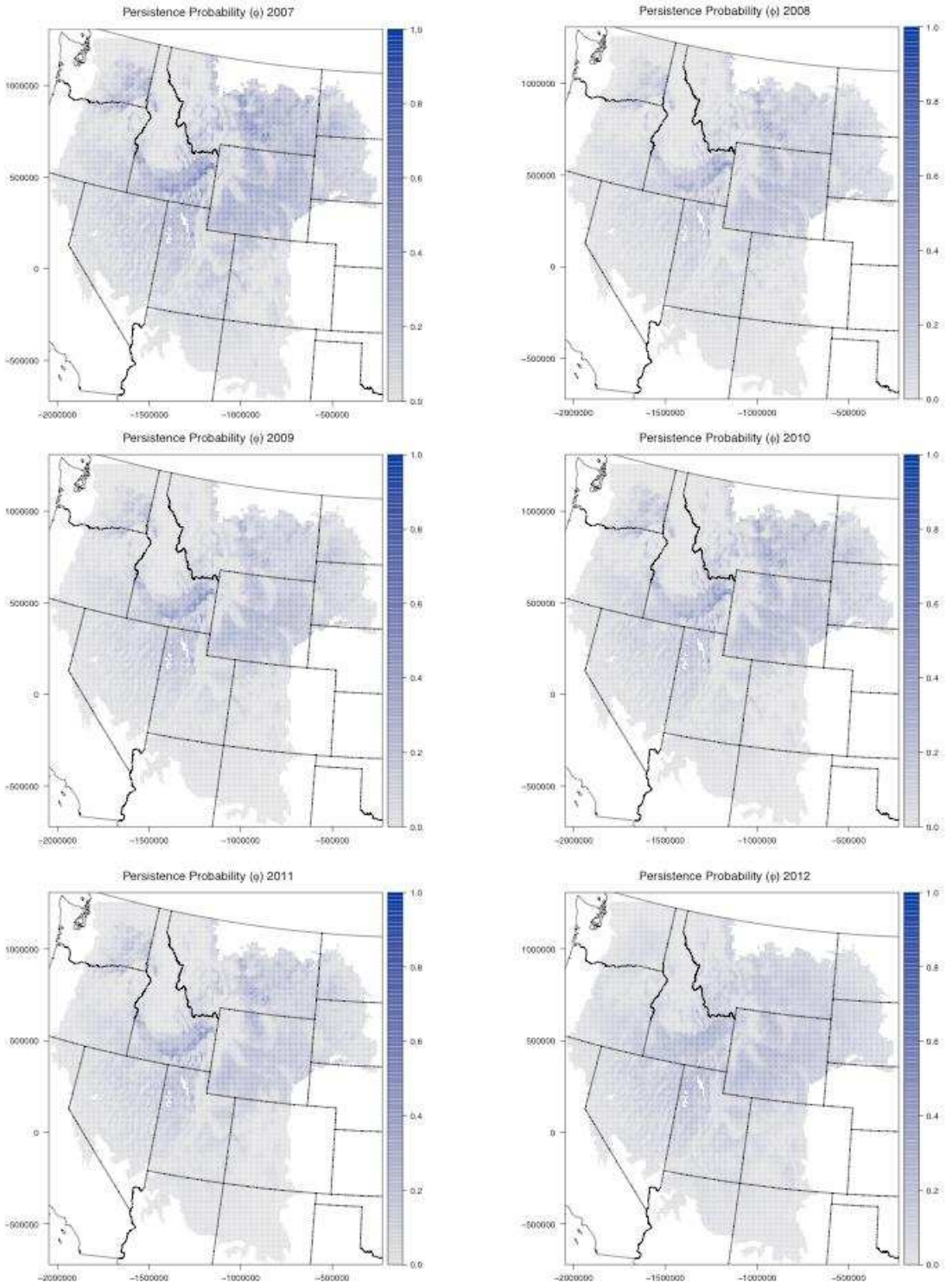

Figure 3.5. Spatial predictions of persistent site-use probability ($\boldsymbol{\phi_{i,t}}$) using mean posterior coefficient estimates. Points represent eagle detections.

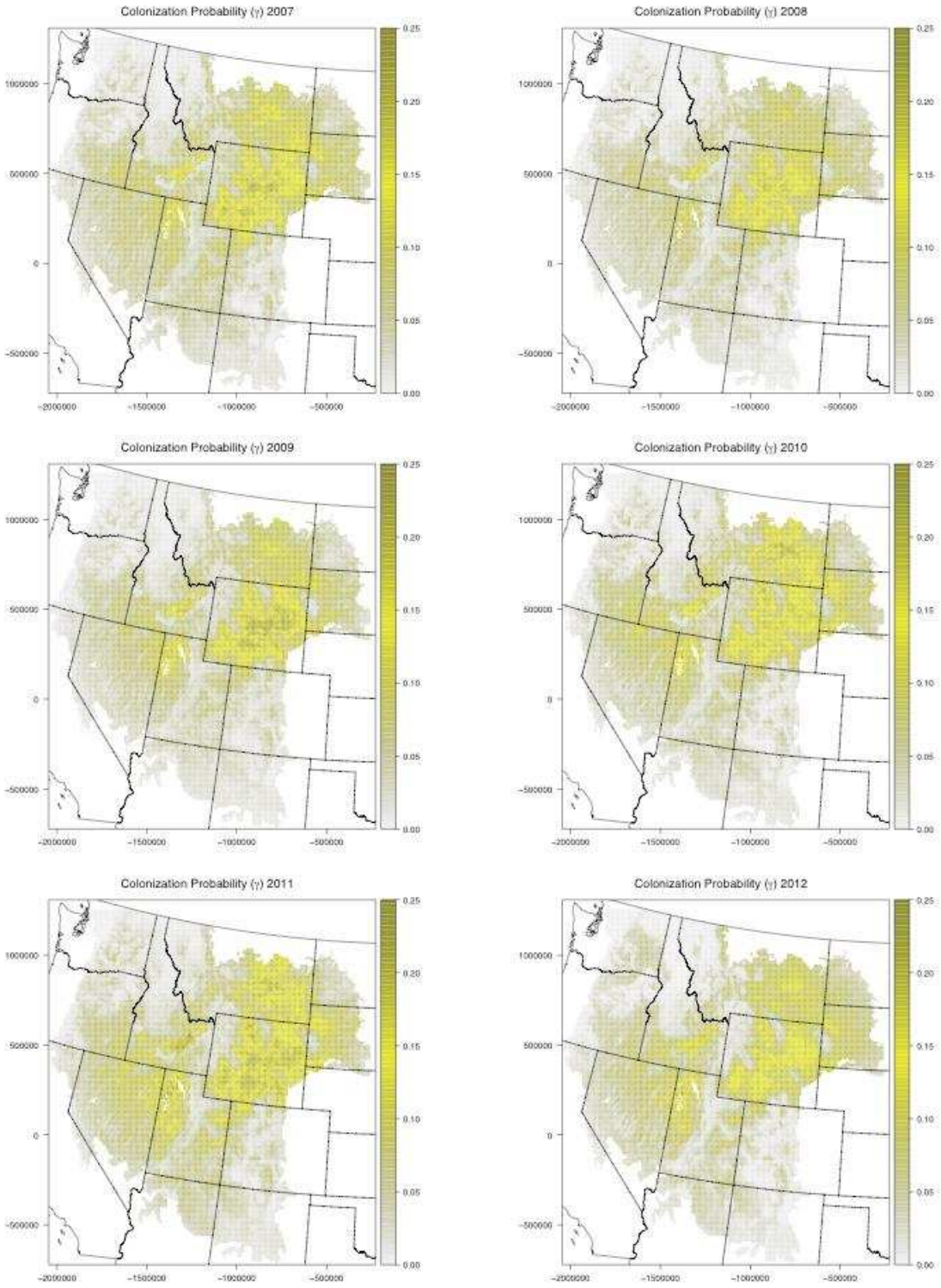

Figure 3.6. Spatial predictions of site colonization probability ($\boldsymbol{\gamma_{i,t}}$) using mean posterior coefficient estimates. Points represent eagle detections.

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Chapter 4: Examining potential bias and power to detect occurrence when applying occupancy analyses to point-transect data.

Point transects are a widely applied sampling method to monitor animal populations. By recording distances from an observer to each detected animal, it is possible to estimate species density via distance sampling. However, the number of detections required to fit detection functions is often prohibitive, and it is common to reduce count data to detection/non-detection data for use in occupancy analyses. Occupancy analyses assume no unmodeled heterogeneity among parameters; yet variation arising from abundance and detection as a function of distance to observer are two sources of heterogeneity that may induce bias when applying binomial models to point count data. We used simulation to investigate patterns of bias and coverage when detection declines with increasing distance from an observer. Applying commonly used methods to estimate occupancy including logistic regression, occupancy analyses, and a Royle & Nichols (Royle and Nichols 2003) abundance-induced heterogeneity estimator revealed that bias pervades all approaches when true occupancy is low and detection declines quickly as a function of distance. Increasing the number of surveys per site has the potential to increase coverage to detect true patterns of occurrence, yet bias remains inescapable. Applying methods to an empirical dataset of avian point transect counts across pinyon-juniper removal treatments in western Colorado, USA revealed that: i) inference on patterns of occurrence and resulting community rankings can shift; and ii) inferences to the magnitude of treatment effects identified using model selection are sensitive following restricting the spatial bounds of analyses in efforts to eliminate bias. We recommend that practitioners use caution when selecting a sample unit for occupancy analyses, and provide simulation code that may be useful in power analyses.

INTRODUCTION

Accurate estimates of the abundance and distribution of animal populations is central to the field of ecology, and of critical importance for conserving and managing wildlife populations. Abundance is perhaps the most common state variable referenced by ecologists and practitioners because it contains the most information among static population metrics. Methods to estimate animal abundance including mark-recapture (Seber 1982), distance sampling (Buckland et al. 2005), removal methods (Skalski and Robson 1982), and count-based regression (Thogmartin et al. 2004), have all received considerable attention in methods publications (Nichols et al. 2009), underscoring the importance of estimating population size in ecology and conservation. Yet population size remains an elusive parameter to accurately estimate with high precision in fish and wildlife studies, particularly when data are limited and inference is desired at large spatial and temporal scales (Noon et al. 2012). In particular, the random variable associated with abundance estimators (i.e. counts, recaptures, distance, etc.) is often difficult or costly to acquire for many organisms; and, accounting for imperfect detection, geographic and demographic closure, and other model assumptions can further complicate estimation (Nichols et al. 2009). In turn, species occupancy—the probability of a species presence at a particular site—offers a more efficient state variable to estimate (Noon et al. 2012).

Occupancy analyses based on detection/non-detection data have seen rapid growth in field studies, and are characterized by a proliferation of analytical methods and applications across diverse fields within ecology (*see* Bailey *et al.* 2014). Determining the presence of a species is often far more practical and cost-effective than obtaining counts or marking individuals, and repeatedly visiting at least some sites provides a flexible framework for

estimating occurrence probability in the face of imperfect detection (Hoeting et al. 2000, MacKenzie et al. 2002, Tyre et al. 2003). Thus, it is not surprising that land management agencies commonly employ occupancy estimation to monitor wildlife populations over large spatial and temporal scales (Manley et al. 2004).

For many avian species, point transects are a common sampling design used to survey and monitor populations (Ralph et al. 1995). During point count surveys, observers estimate the distance from the point to each detection. The random variable in this case is the distance to an individual detection. The frequency distribution of distances to detected individuals is assumed to decline monotonically with distance from the point. Fitting a detection function to these data (e.g., half-normal) allows researchers to estimate detection probability as a function of distance from the point and the overall proportion of individuals detected within a fixed radius from the point. Density is estimated by dividing the total count by the detection probability over the survey area (Buckland and Handel 2006). Other methods which aim to estimate density without using distance data to estimate detection parameters include independent (Alldredge et al. 2006) or dependent (Nichols et al. 2000) multiple-observers , time-to-detection methods (Farnsworth et al. 2002), or replicate counts (Royle 2004). For distance-based methods, the number of detections required to fit detection functions (n >60; Buckland *et al.* 2005) is often prohibitive, particularly when species are rare or sampling efforts are limited. Furthermore, in terms of bias, non-distance-based density estimators have been demonstrated to offer little advantage over uncorrected methods (Efford and Dawson 2009). As such, it has become common for researchers to reduce count data to detection/non-detection data and estimate occupancy rather than abundance or density. This has occurred, for example, in studies of community dynamics (Ruiz-Gutiérrez et al. 2010), species response to management or disturbance (Bayne et al. 2008),

or in support of land use planning (Odell et al. 2003). Studies often take advantage of repeated surveys to estimate detection probability (MacKenzie 2006), or dismiss the importance of imperfect detection and estimate occurrence without accounting for non-detections (Hutto and Young 2002, Mac Nally et al. 2008).

Information on species occurrence is provided by point transect count data whenever the count for a given species is >0. However, applying occupancy methods, which require at least some sites be surveyed more than once, to count data can result in: i) abundance-induced heterogeneity in the detection process (Royle and Nichols 2003); and ii) distance-induced heterogeneity among detections (McClintock et al. 2010a). Failing to account for these sources of variation in the detection process is synonymous with failing to meet the assumptions of most ecological models, ultimately resulting in biased estimates (Miller et al. 2015). Occupancy methods can model heterogeneity at the level of replicate surveys; however, there are currently no methods to adjust for heterogeneity at the level of detections (Miller et al. 2015). Thus, variation in detectability as a function of distance to the observer is tantamount to individual variation in detection when organisms are detected at varying distances.

We conducted a simulation study to evaluate the magnitude and direction of any biases which may arise when point count data are reduced to occurrence (binary) data and the distance-to-detection information is ignored. By varying the shape of monotonically declining detection functions, the number of repeat visits, and the true occurrence probability, we generated datasets arising from: i) varying the spatial distribution of individuals arising from a random spatial point process model; and ii) an imperfect detection process. We fit commonly employed models used to estimate occurrence probability to simulated datasets. We then applied our findings to an empirical study of avian occurrence in response to the mechanical removal of pinyon-juniper

woodlands using avian point count data collected from 2012-15 in the Piceance Basin of northwest Colorado, USA. The goals of our research were to provide practitioners with a rigorous evaluation of these commonly applied estimators assumed to produce unbiased estimates of occupancy, a critical state variable for the conservation and management of many wildlife populations. Lastly, we provide R code such that practitioners can evaluate the potential of biases in field studies where detecting organisms declines with increasing distance.

METHODS

Simulated Data and Analyses

We sought to recreate typical point transect datasets for use in occupancy analyses using a "virtual ecologist" framework (Zurell et al. 2010). Our aim was to better identify situations where occupancy analyses can and cannot reliably applied to point transect data (citation) by generating: 1) the ecological process of avian point locations; and 2) a sampling process that can produce heterogeneous false negatives by observers failing to detect individuals present on a site. Investigating the ecological and sampling scenarios, which give rise to field data allowed us to explicitly evaluate the inferential consequences of violating model assumptions. While we use birds as an example to frame our simulations, we intend for our analyses and inference to be transferable to any organism surveyed by point transects (Weir et al. 2005).

Each simulation began with a sampling frame that consisted of N=400 potential sites to be surveyed (20x20 grid of sites). Each site was a square, with 200m on a side (Ralph et al. 1995). To populate the sampling frame with bird abundances, we generated a random number of birds for each site following a Poisson distribution, and randomly placed individuals within the

site if a random number >0 was generated. Given occupancy (ψ) as our state variable for subsequent analyses, we derived intensity parameters for the Poisson distribution (λ) generating counts of birds from the probability of occurrence $\left(Pr(\lambda > 0);\ \lambda = -\log(1-\psi)\right)$. We considered five levels of occurrence across simulations, corresponding to bird species that may occur as relatively rare to ubiquitous using ψ = 0.1, 0.3, 0.5, 0.7, and 0.9 (λ = 0.105, 0.357, 0.693, 1.204, and 2.303, respectively). Once bird locations were generated for a given simulation across the sampling grid, we calculated true occupancy as the mean number of sites containing at least one bird.

For the sampling process, we employed simple random sampling for each simulation to select n=60 sites (i) among the 400 available in the sampling frame. We placed a point count station at the center of each sampled site to simulate the process of probabilistically detecting birds within the site. Figure 4.1 provides an example of a sampling frame used when generating datasets for analyses.

Given that a site was occupied (# birds > 0), we assumed that the probability of detection declined as a function of distance from the observer following a half normal distribution (Buckland et al. 2005). Thus, a bird was considered detected following a Bernoulli distribution with probability conditional on the distance (d) from each bird to the observer, and the shape parameter (σ) from the half normal probability density function.

$$\text{Bernoulli}\left(exp\left(-\frac{d^2}{2\sigma^2}\right)\right)$$

Detecting an organism in field studies will vary by attributes specific to the species and the ability of the observer (Simons et al. 2009). For example; size, coloration and pattern give rise to heterogeneous detection for visually detected individuals (Buckland et al. 2001); whereas

for species detected by aural cues, frequency, pitch, and volume converge to influence an observer's ability to detect an individual (McClintock et al. 2010a). Furthermore, variation in local (e.g. site) abundance induces heterogeneity in the probability that ≥ 1 individual is detected (Royle and Nichols 2003). We did not simulate these sources of heterogeneity in cue detection—rather, we simply assumed that no individual within a site was perfectly detectable beyond 0 distance from an observer. Our focus was on the performance of estimators as the variation among detection ranged from inconspicuous or inaudible to seen or heard with high probability. The maximum distance from the observer to a bird was 141.4m given 200m square sites (Figure 4.1), so we chose values of σ = 30, 50, 70, 90, and 110 to capture likely variation in detectability across species typically encountered among sample plots (Figure 4.2). Across simulations, we assumed that observers were similar in ability and training and we did not model heterogeneity among observers (Scherer et al. 2012).

Repeat visits to sites generally increase the number of individuals detected, providing better estimates of detection functions used to derive density estimates (Buckland et al. 2005), and are necessary to estimate detection probabilities from occupancy surveys (MacKenzie et al. 2002). At a minimum, we considered that each station in the sample would be surveyed twice ($j = 2$), and also considered scenarios with three or four replicate visits to each site. Bird locations for each site did not change between repeated visits, reflecting static spatial distributions for territorial individuals during the breeding season.

We simulated 500 datasets (s) for each combination of occupancy (ψ), detection function (σ), and number of replicate surveys (j), resulting in 75 parameter combinations and 37,500 datasets. Each dataset contained a total count of birds for each site and repeated survey, from which data were truncated to binary data for analyses.

Model Fitting and Estimation

We fit occupancy models commonly applied to point transect data. The underlying probability model for binary ecological data is the binomial probability distribution. Well-established methods have been developed to address zero-inflation (i.e., false negatives) arising from imperfect detection (Hoeting et al. 2000, MacKenzie et al. 2002, Tyre et al. 2003), and abundance-induced heterogeneity in the detection process (Royle and Nichols 2003). We applied the most common analytical techniques to presence-absence data including: i) logistic regression (*LR*); ii) a 'single-season' occupancy model (MacKenzie 2006); and the iii) Royle & Nichols (*RN*; 2003) abundance-induced heterogeneity model. In the RN model occupancy probability is derived following an estimation of a mean population size.

To fit the LR model, we truncated repeated surveys across datasets for each site such that $y_i = 1$ if ≥ 1 individual was detected on at least one survey, and $y_i = 0$ otherwise (Table 4.1). We used maximum-likelihood to estimate the probability of occurrence, using the glm package in program R (R Core Team 2014). We recognize that applying logistic regression to detection/non-detection data does not directly estimate occupancy, but rather occupancy conflated with detection. However, because accurate estimates of an ecologically meaningful parameter is the intent in most studies using LR, we will use the term "occupancy" to remain consistent with the published literature.

We used a hierarchical Bayesian parameterization to estimate occupancy and detection probabilities for OCC and RN models. A Bayesian approach for OCC and RN simulations allowed us to fit models that would sometimes fail to converge, or produce unreasonable measures of precision when parameters were near the bounds of 0 or 1 using maximum-likelihood methods (J Tack, unpublished data). We estimated the latent true occupied state of

each site (z_i) assuming a Bernoulli distribution with a constant probability of occurrence (ψ). Detections (y_i) arise from a Binomial likelihood with detection probability (p) over J_i replicate surveys when a site is occupied ($z_i = 1$).

$$y_i \sim \begin{cases} 0 & \text{when } z_i = 0 \\ \text{Binomial}(J_i, p) & \text{when } z_i = 1 \end{cases}$$

$$z_i \sim \text{Bern}(\psi)$$

For OCC and RN analyses we reduced survey specific positive counts to $y_{i,j} = 1$, and summed across repeated surveys (Table 4.1). We assumed vague prior Beta (α =1, β = 1) distributions on unknown parameters for detection and occupancy probability. However, in many field studies prior knowledge about species occurrences may be available to inform prior distributions.

Lastly, we fit a model developed by Royle & Nichols (2003) using a similar binomial distribution. However, in the RN model detection probability at a given site (p_i) is derived from an individual detection probability (r) and the local abundance (Ni) at site i where N_i is assumed to follow a Poisson distribution.

$$p_i = 1 - (1 - r)^{N_i}$$

Under the RN parameterization, occupancy probability is derived from the intensity parameter of the Poisson probability mass function (λ_i)—the probability that $N_i > 0$ at site i ($\psi_i = 1 - \exp(\lambda_i)$). Again, we assumed vague priors for the individual detection probability $\left(r \sim \text{Beta}(1,1)\right)$ and the intensity parameter $\left(\lambda \sim \text{Gamma}(.001, .001)\right)$.

We fit each model using Markov Chain Monte Carlo (MCMC) sampling (OCC, RN) and ran 3 chains each with 10,000 iterations to estimate posterior distributions, discarding the first 2000 iterations as burn-in. To examine convergence of posterior distributions (Gelman and Rubin 1992), we calculated the Gelman-Rubin convergence statistic for each MCMC analysis.

We fit each model, other than LR, employing MCMC sampling for computational purposes, and used readily available algorithms (MacKenzie 2006)(Fiske and Chandler 2011).

For each simulation we estimated occupancy probability for each model (m) and simulation (s; $\hat{\psi}_{m,s}$) using either maximum likelihood (LR), or the mean of posterior distributions (OCC, RN), and calculated proportional bias as $\left(\frac{\hat{\psi}_{m,s}-\psi_s}{\psi_{,s}}\right)$ where ψ_s was truth for a given simulation. We also calculated coverage as the proportion of simulations for each model that contained the true parameter estimate within the 95% credible interval for Bayesian methods (OCC, RN), or 95% confidence interval (assuming asymptotic normality) for LR. Lastly, we calculated a metric similar to the coefficient of variation, by dividing one fourth of the range of 95% CR or CI by the mean of each estimate.

Empirical Data and Analyses

The Piceance Basin in northwest Colorado ranges in elevation from 1700 to 2700m, and is dominated by pinyon-juniper woodlands and sagebrush (Sedgwick 1987). Point count stations were located within three treatments classes including: 1) sites where trees were removed, > 40 years prior to surveys, by dragging chains through pinyon-junipers woodlands (Aro 1971); 2) sites with recent (2013) tree removal by means of chopping and mulching of standing vegetation ("hydoraxing"); and 3) reference stations with intact pinyon-juniper woodlands (Figure 4.3). In total, technicians surveyed 25 point count stations dispersed within each of the removal treatment groups, and 50 stations randomly placed within undisturbed pinyon-juniper woodlands for a total of 100 sampling stations.

At each station, five-minute point count surveys (Dunn et al. 2006) were conducted four times during spring field seasons (April-June) from 2013-2014. Two to three observers alternated between each site. All surveys were conducted between 30 minutes after sunrise to

mid-morning, and were not conducted during periods of fog, rain or high winds (Ralph et al. 1995). Observers noted all birds detected during surveys, and estimated the distance from the observer to the detection using rangefinders. Observation-specific covariate data (i.e., observer, time of survey, wind gusts, and cloud cover) were also collected.

We fit three model types (LR, OCC, RN) to species-specific occurrence data from 2014 for five species encountered during the surveys using detections out to 250m, resulting in a site of ~19.6ha. Using treatment as a categorical covariate, we fit all possible combinations of null or treatment effects on occupancy (LR, OCC, RN) and detection (OCC, RN) probabilities. Because preliminary analyses indicated that observer and weather effects were unrelated to detection probability (T Gallo unpublished data), we did not model these effects. We used R package unmarked to obtain maximum likelihood (ML) estimates for OCC and RN models (Fiske and Chandler 2011). We chose ML methods for empirical analyses so that we could AIC model selection to compare models across LR, OCC, and RN (Burnham and Anderson 2002). We distinguished among a maximum of four models representing hypotheses involving treatment effects on songbird occurrence and detection probabilities (Burnham and Anderson 2002). For RN models, we derived occupancy from mean estimates of local population size using methods described above.

We combined all detections from 2013 and 2014 to fit a half-normal detection model to distance data for each species using the R package unmarked (Fiske and Chandler 2011), and used estimates of $\hat{\sigma}$ (shape parameter) from the fitted detection function to rank species from lowest to highest detectability. Using the estimate from $\hat{\sigma}$ of the lowest detected species, we calculated the effective radius of detection ($\hat{\rho} = \sqrt{2\hat{\sigma}^2}$) which represents the distance at which as many detections beyond ρ are detected, as are missed within ρ (Buckland et al. 2005). Using

this value, we truncated occurrence data for all species to only include detections recorded within the effective radius of detection for the lowest detectable species, and repeated occurrence analyses outlined above. We reasoned that limiting the size of the sample unit minimized the likelihood of false negatives (McClintock et al. 2010a), and standardized the size of the sample unit for comparison of occupancy estimates.

RESULTS

Simulations

Each estimation method we explored produced biased estimates under different scenarios; however, failing to account for imperfect detection (model LR) consistently produced the most biased estimates of occupancy (Figure 4.4). Biases were consistently negative across methods because occupancy is underestimated with increasing false negative rates (Figure 4.4). Biased estimates were pervasive across algorithms when detection probability decayed quickly with distance ($\sigma < 70$), and were more variable with low levels of occupancy or local site abundance. Estimates from RN models exhibited the lowest bias among methods considered yet consistently resulted in estimates with low precision (Figure 4.5). When detection decayed quickly with distance ($\sigma = 30$), coupled with low levels of occupancy ($\psi = 0.1$), each method displayed the highest and most variable bias across simulations suggesting that rare and cryptic species may be the most vulnerable to biased estimates when applying occupancy estimation to point count data. Conversely, as the value of σ increased such that there was little heterogeneity in detection within a site, each method was capable of producing unbiased estimates of occurrence.

Increasing the number of visits to each site from two to four had minimal effects on decreasing bias in ψ-estimates (Figure 4.4). In theory, organisms with detection probabilities > 0 would eventually be detected with enough trials, but a large number of surveys is infeasible for most studies. However, the mean bias and precision of estimates were reduced as the number of visits increased (Figure 4.5). LR methods consistently produced the most precise estimates of ψ because one fewer parameter was estimated from the data. However, because LR methods fail to account for uncertainty in the observation process, their precision is misleading. The deficiency of LR methods is revealed by their poor coverage—estimates of ψ contained truth within their bounds of uncertainty < 0.5 of the time even when number of surveys or occurrence levels were increased (Figure 4.6).

Coverage across estimation methods was most sensitive to variation in detectability (Figure 4.6). For the species with little variation in detection probability ($\sigma = 110$), all methods included truth within the bounds of estimated uncertainty for at least 95% of simulations. However, as detectability declined, coverage also declined to the point that coverage was almost zero for simulated species with low detectability ($\sigma = 30$) and two replicate surveys. Increasing survey effort from two to four visits increased coverage for methods that jointly estimated occurrence and detection (RN and OC). RN methods benefitted from greater coverage than occupancy methods, yet with high occurrence and low detection, the observed coverage across methods may not be acceptable to practitioners.

Empirical Analyses

The Piceance Basin data set consisted of 5,669 observations of 73 species (T Gallo unpublished data). We restricted our analyses to a set of species with sufficient data to estimate distance-based detection functions (> 200 detections). We chose five species including rock wren (*Salpinctes obsoletus;* ROWR), white-breasted nuthatch (*Sitta carolinesis*; WBNU), spotted towhee (*Pipilo maculatus;* SPTO), blue-grey gnatcatcher (*Polioptila caerulea*; BGGN), and chipping sparrow (*Spizella passerine*; CHSP).

Using data from 2013-2014 to fit half-normal distributions to their detection data produced estimates of $\hat{\sigma}$=37.2 (SE=1.08), 46.7 (1.28), 58.9 (1.92), 63.3 (1.37), and 101.0 (3.34) for BGGN, CHSP, WBNU, SPTO, and ROWR, respectively. All estimates fell within the bounds of values we simulated, and each species had a sufficient number of detections to estimate density via distance sampling algorithms. After fitting species-specific LR, OCC, and RN models using a 250m radius to around point count stations, we also fit models in light of an estimate of effective radius of detection for the BGGN, the most cryptic species considered ($\hat{\sigma}$=37.2, $\hat{\rho}$=52), by using a 50m radius around stations.

Based on AIC model selection, the most parsimonious model was sensitive to the model-fitting algorithm employed (Table 4.2; Full model selection results available in Appendix 4.1). It is important to remember that LR methods do not adjust the data for uncertainty in the observation process, and, as a result, leads to improper inference when there is heterogeneity in the detection process (i.e. $\psi = \psi * p$). When considering the full dataset, the top models included an effect of treatment on occurrence for each species except SPTO and heterogeneity in the detection process (OCC, RN) for ROWR and CHSP. Truncating the dataset to remove potential biases due to unmodeled variation in detection for OCC and RN methods revealed

inconsistent top models identified for each species except BGGN. For example, treatment effects on occurrence may have been inconspicuous (ROWR) or overstated (WBNU, CHSP) contingent on the spatial scale and associated bias of analyses (Table 4.2).

Because the sample sites became smaller for truncated datasets, estimates of occurrence understandably differed between analyses using full and truncated datasets. Occurrence estimates for some combinations of species, treatments, and models demonstrated the potential to change by an order of magnitude (Table 4.3). Intuitively, occupancy should decrease in concert with decreasing site size, as smaller units should be concomitantly less likely to contain at least one individual (Efford and Dawson 2012). However, the point estimates of the WBNU actually increased following site truncation using OCC and RN methods (though with decreased precision; Table 4.3), suggesting that negative bias may have resulted in underestimating site occupancy prior to truncation.

DISCUSSION

We simulated point transect data that reflect two common sources of variation in the observation process: abundance induced heterogeneity (Royle and Nichols 2003), and an increasing rate of false-negatives at farther distances from observers (McClintock et al. 2010a). These two sources of heterogeneity—abundance and distance-induced—are often inappropriately ignored when raw count data are used in estimates of occupancy. Based on data that simulated the ecological and sampling processes common to bird surveys, we found that estimates of occupancy could be severely biased, particularly for scenarios where detectability is low relative to the plot size. One method we tested, RN, explicitly accounted for site-level,

abundance-induced heterogeneity and this method resulted in the least biased estimates among methods we compared. To our knowledge, the RN model has received little attention as a derived parameter in occupancy studies (Pusparini and Wibisono 2013). However, our simulations demonstrate that occupancy estimates with the RN model are the most imprecise, an outcome exacerbated when detectability is low.

Ignoring imperfect detection, as in LR models, resulted in the highest proportional bias among the models we explored. Only when one assumes that detectability is relatively invariant across sample surveys (e.g., as in an index; σ=110, j=4 in our simulations), are the occupancy estimates from LR comparable to methods that account for imperfect detection. However, it is our inclination that in multi-species wildlife surveys it would be difficult to defend an a priori assumption of no heterogeneity in the detection process. Therefore, the desirable property of increased precision in LR estimates is negated by the bias that's inherent in the data that do not account for an imperfect observation processes. For LR estimates, this deficiency was highlighted by the poor coverage among simulations when detectability and occurrence were low, a problem that was not alleviated even with an increased number of repeated surveys per station.

Occupancy analyses appear to invoke a pronounced trade-off between reducing bias and increasing the precision of the estimates. An important insight provided by our simulations was the observation that unbiased estimates of occupancy were almost impossible to obtain when detectability was low. In addition, detection heterogeneity arising from the decay in detectability as a function of distance from the observer has been found to result in negatively biased estimates of occupancy (McClintock et al. 2010a). This source of bias, which is often ignored in practice, is exacerbated at low levels of occupancy across all analytical methods. As a result,

estimates of occupancy for rare and inconspicuous species, often species of greatest conservation concern, are most likely to result in biased estimates.

We extended our simulation analyses to include an empirical dataset where data collection followed a typical point transect survey design used by land management agencies. Federal land management agencies, such as the U.S. Forest Service, are legally required to minimize the adverse effects of their management practices on plant and animal diversity (Schultz et al. 2013). These agencies often assess their impacts on bird communities, for example, by conducting occupancy surveys as part of a long-term monitoring program (Noon et al. 2012). This legal requirement underscores the importance of accurate estimates of occupancy. The scale parameters (σ) we estimated, based on pooling two years of field data, revealed that multi-species surveys typically encompass a wide range of detectabilities, similar to those we simulated. It is our opinion that even highly qualified and competent filed biologists cannot account for this source of detection heterogeneity during the data collection process.

Relative occupancy, or incidence, with a species assemblage is often of interest to community ecologists (Preston 1948, Diamond 1975). However, deriving unbiased estimates of relative occupancy rates in a multi-species context is difficult because the estimation process is inescapably accompanied by detection heterogeneity. Heterogeneity arises for at least two reasons: 1) species inherently differ in their detectabilities because behaviors such as vocalization intensity and frequency of cue production vary extensively by species; 2) species occur at different densities with the study area and, as a result for a fixed plot size, abundance-induced heterogeneity is almost unavoidable. Occupancy is most likely to be negatively biased for rare (low density) species with cues that are infrequent or difficult to detect. Our simulations clearly revealed that these sources of bias are likely to occur in most community level bird

studies. Increasingly, occupancy analyses are being used by land management agencies as an efficient strategy for monitoring multiple species across large spatial areas (Noon et al. 2012). If point counts are employed for community monitoring, researchers should careful evaluate the effects of plot size on occupancy estimates and perhaps consider adopting variable plot sizes to reflect species-specific differences in space-use.. in selecting site dimensions when there are differences in ability to detect species of interest. In particular, focusing on the least detectable species should be a priority.

Unfortunately, there is currently no method to estimate occupancy that accounts for variation in the observation process using existing model-based solutions. Model extensions that incorporate individual variation in detection estimated, for example, from distance-based sampling schemes, are needed to achieve unbiased estimates of occupancy. Until then, using design-based approaches to limit the degree of heterogeneity among individuals within a species, and across species, may be the best that can be done at this time (Hutto and Young 2002, McClintock et al. 2010b). We suggest for consideration an interim design feature for multi-species occupancy estimation—restricting the size of the sample unit to the effective detection radius of the least detectable species. However, this approach also has limitations because these species often have insufficient data for estimating their detection functions. A partial solution is to borrow detection information from more abundant species with similar detection probabilities based on attributes of cue production.

To aid in the design of field studies with the goal of minimizing the potential for bias in occupancy estimates, we provide computer code to reproduce our simulations with applications specific to their research. This tool may also be useful for power analyses, and sampling

decisions when balancing effort between sample size and number of replicate surveys (Bailey et al. 2007).

TABLES

Table 4.1. Three examples of simulated bird counts with j=3 repeated visits, and resulting data structure for analyses using logistic regression (LR), and occupancy analyses (OCC), and the Royle-Nichols (RN) estimator using a binomial probability model. LR data is estimated using maximum likelihood from binary data; OCC and RN methods use a binomial probability distribution of y_i successes of j trials.

Simulated counts (j=3)	LR	OCC	RN
0 0 0	0	0	0
5 2 0	1	2	2
3 1 2	1	3	3

Table 4.2. Model selection results displaying structure (treatment vs null) identified on occurrence (ψ) and detection (det) from most parsimonious model ($\Delta AIC_c = 0$). Separate models including occupancy (OCC), Royle-Nichols (RN), and logisitic regression (LR) were fit to each species considered in analyses. Detection parameters are specific to the site (p_i) for occupancy models, individuals (r_i) for RN models, and not estimated for LR models. Species are ordered from estimated lowest detectability (σ=37.2; BGGN) to highest (σ= 101; ROWR).

Species	Model	Full Dataset		Truncated (50m)	
		ψ	det	ψ	det
BGGN	OCC	treatment	(.)	(.)	treatment
	RN	treatment	(.)	treatment	(.)
	LR	treatment	NA	treatment	NA
CHSP	OCC	treatment	treatment	(.)	treatment
	RN	(.)	treatment	(.)	treatment
	LR	treatment	NA	(.)	NA
WBNU	OCC	treatment	(.)	(.)	(.)
	RN	treatment	(.)	(.)	(.)
	LR	treatment	NA	treatment	NA
SPTO	OCC	(.)	(.)	(.)	treatment
	RN	(.)	(.)	(.)	treatment
	LR	(.)	NA	(.)	NA
ROWR	OCC	(.)	treatment	(.)	(.)
	RN	(.)	treatment	(.)	(.)
	LR	treatment	NA	(.)	NA

Table 4.3. Point estimates and 95% CI from top model across species and analyses methods.

Model	Spp	Chaining		Hydroax		Reference	
		Full	50m	Full	50m	Full	50m
Occ	BGGN	0.94 (0.22-1.00)	0.74 (0.51-0.88)	0.54 (0.31-0.76)	0.74 (0.51-0.88)	0.77 (0.54-0.90)	0.74 (0.51-0.88)
	CHSP	1.00 (0.00-1.00)*	0.76 (0.42-0.93)	1.00 (0.00-1.00)*	0.76 (0.42-0.93)	0.70 (0.45-0.88)	0.76 (0.42-0.93)
	WBNU	0.39 (0.20-0.62)	0.70 (0.09-0.98)	0.53 (0.30-0.75)	0.70 (0.09-0.98)	0.70 (0.50-0.85)	0.70 (0.09-0.98)
	SPTO	0.79 (0.69-0.87)	0.49 (0.37-0.61)	0.79 (0.69-0.87)	0.49 (0.37-0.61)	0.79 (0.69-0.87)	0.49 (0.37-0.61)
	ROWR	0.47 (0.34-0.60)	0.25 (0.10-0.48)	0.47 (0.34-0.60)	0.25 (0.10-0.48)	0.47 (0.34-0.60)	0.25 (0.10-0.48)
RN	BGGN	0.96 (0.73-1.00)	0.96 (0.73-1.00)	0.76 (0.43-0.97)	0.76 (0.43-0.97)	0.90 (0.63-0.99)	0.90 (0.63-0.99)
	CHSP	1.00 (0.44-1.00)	0.93 (0.38-1.00)	1.00 (0.44-1.00)	0.93 (0.38-1.00)	1.00 (0.44-1.00)	0.93 (0.38-1.00)
	WBNU	0.48 (0.25-0.77)	0.89 (0.06-1.00)	0.61 (0.37-0.85)	0.89 (0.06-1.00)	0.76 (0.55-0.93)	0.89 (0.06-1.00)
	SPTO	0.83 (0.71-0.92)	0.52 (0.39-0.68)	0.83 (0.71-0.92)	0.52 (0.39-0.68)	0.83 (0.71-0.92)	0.52 (0.39-0.68)
	ROWR	0.49 (0.35-0.65)	0.27 (0.10-0.59)	0.49 (0.35-0.65)	0.27 (0.10-0.59)	0.49 (0.35-0.65)	0.27 (0.10-0.59)
LR	BGGN	0.76 (0.57-0.90)	0.62 (0.43-0.80)	0.15 (0.05-0.37)	0.13 (0.04-0.34)	0.20 (0.07-0.45)	0.20 (0.07-0.44)
	CHSP	0.56 (0.37-0.74)	0.40 (0.49-0.49)	0.54 (0.28-0.79)	0.40 (0.49-0.49)	0.80 (0.54-0.95)	0.40 (0.49-0.49)
	WBNU	0.32 (0.16-0.51)	0.04 (0.00-0.27)	0.45 (0.19-0.74)	0.04 (0.00-0.27)	0.63 (0.35-0.84)	0.04 (0.00-0.27)
	SPTO	0.76 (0.68-0.83)	0.38 (0.30-0.47)	0.76 (0.68-0.83)	0.38 (0.30-0.47)	0.76 (0.68-0.83)	0.38 (0.30-0.47)
	ROWR	0.48 (0.29-0.67)	0.15 (0.09-0.22)	0.34 (0.14-0.61)	0.15 (0.09-0.22)	0.09 (0.01-0.29)	0.15 (0.09-0.22)

*Boundary estimation issues with model-fitting algorithm likely resulted in inflated variance estimate

FIGURES

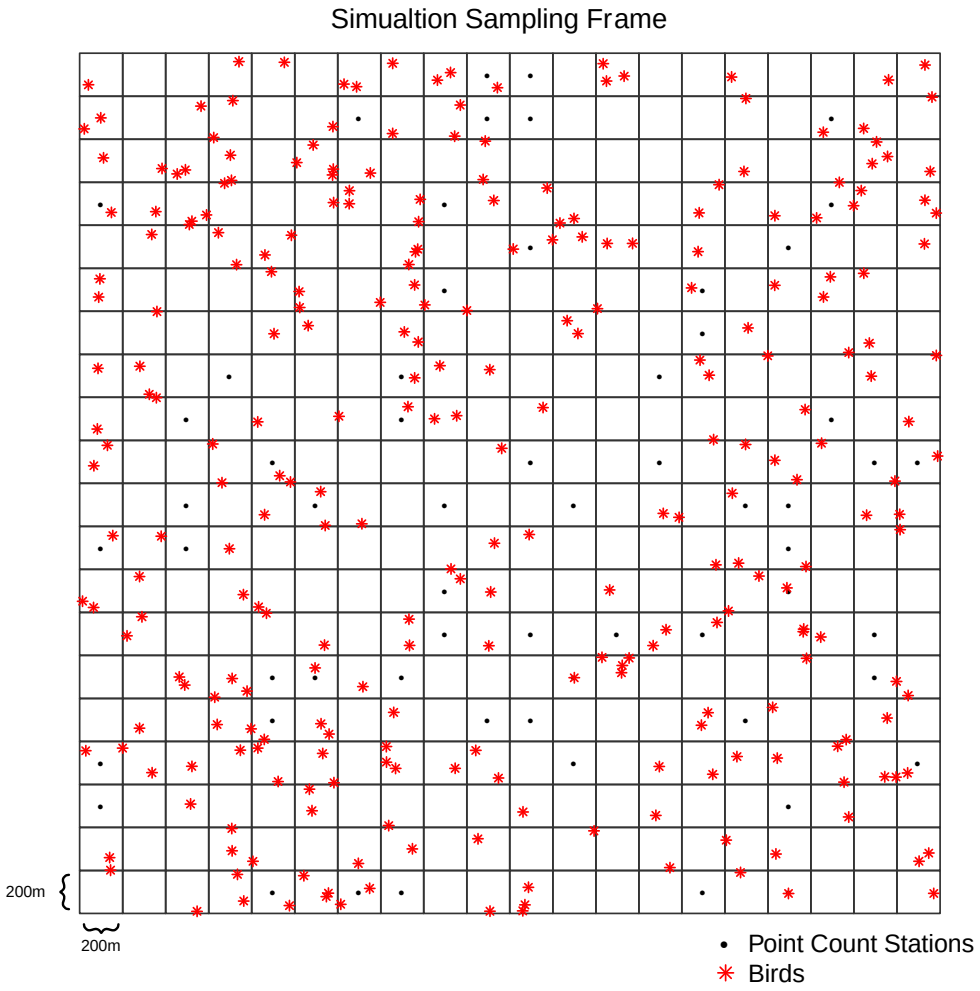

Figure 4.1. Example simulation sampling from consisting of 400 (20x20) sites, each a 200m square. Simple random sampling was used to select n=60 point count stations to be surveyed by an observer 2 to 4 times. This example was generated by drawing a random number (of birds) from a Poisson distribution for each site assuming ψ=0.5 (λ=0.693), and randomly placing birds in sites with non-zero counts.

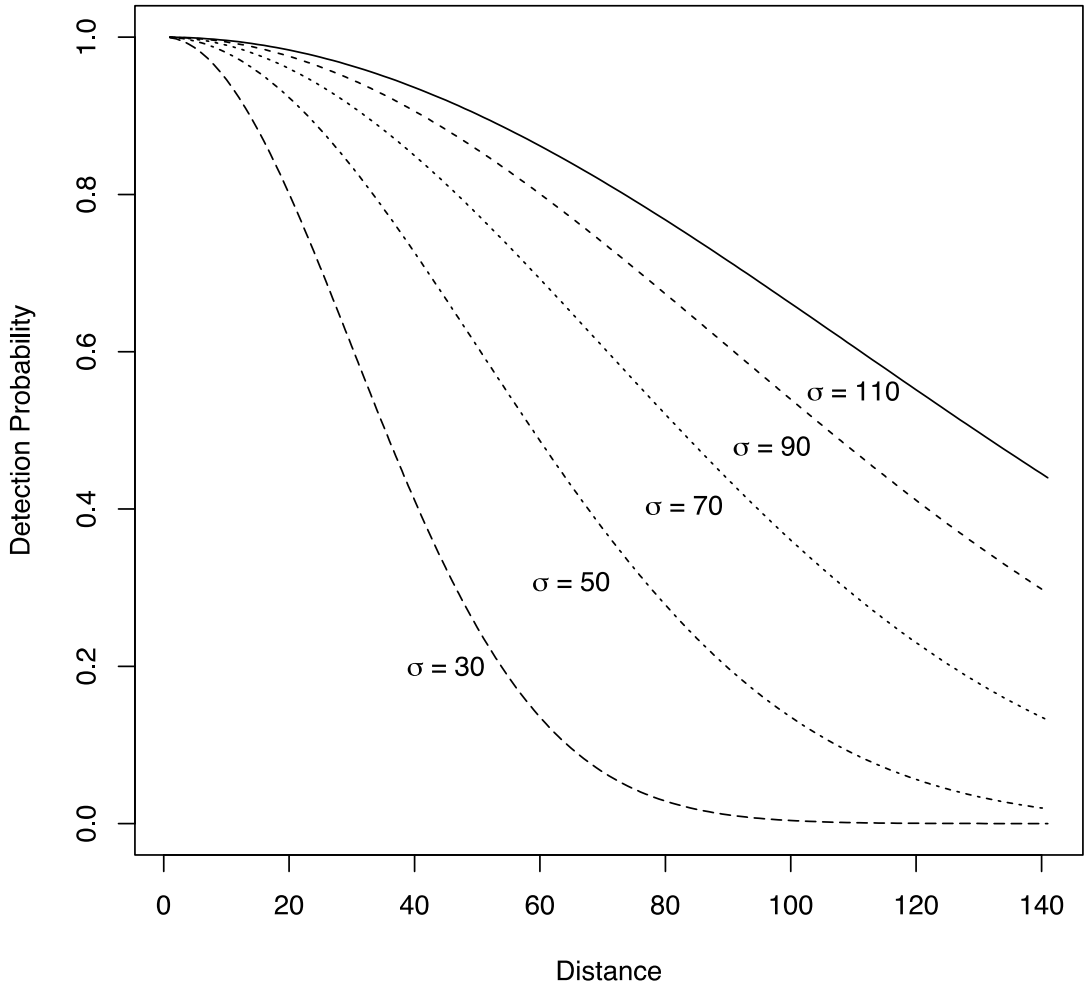

Figure 4.2. Detection functions used to simulate observation process from an observer to each point location within a site. Detection functions follow a half-normal distribution $exp\left(-\frac{d^2}{2\sigma^2}\right)$, with a shape parameters σ= 30, 50, 70, 90, and 110.

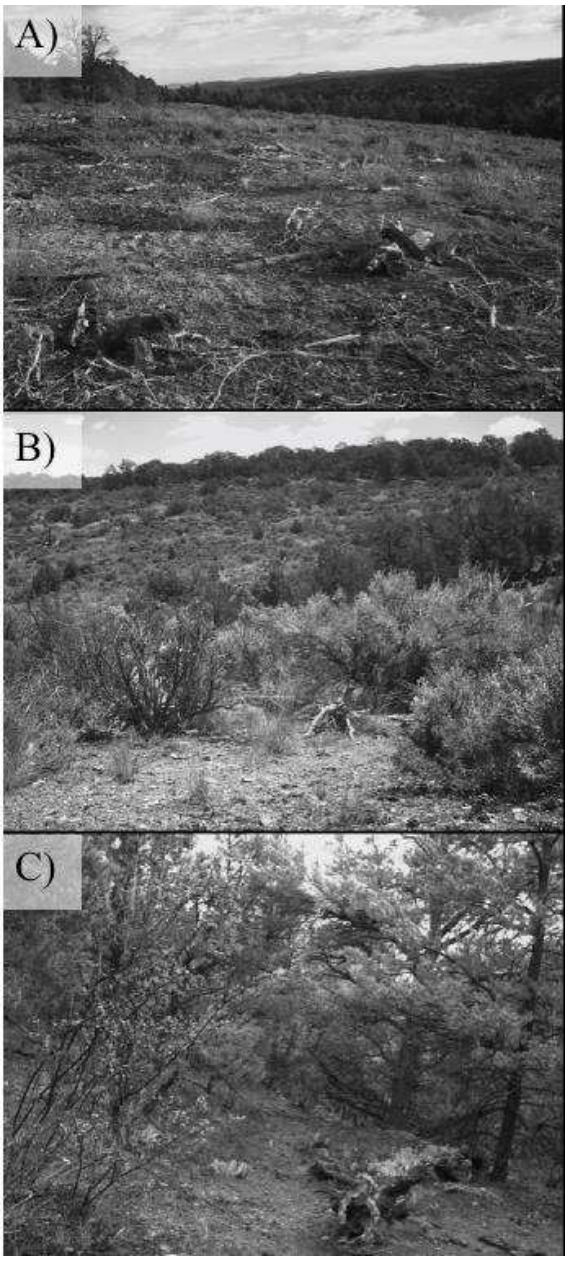

Figure 4.3. Treatment plots for recently remove pinyon-juniper woodlands (PJ) using a hydroaxing technique (A), historically removed PJ from chaining woodlands (B), and (C) reference sites with intact PJ.

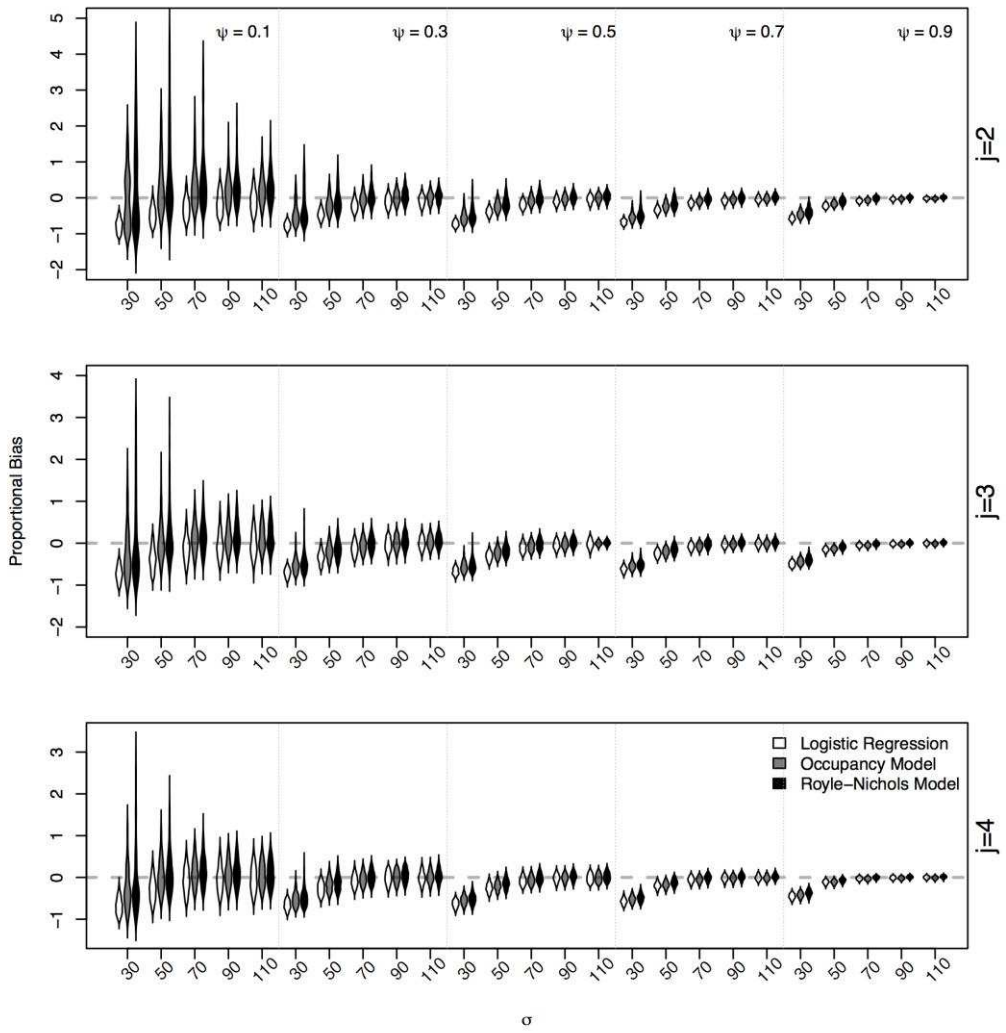

Figure 4.4. Proportional bias calculated across 500 simulations for estimates of occupancy using logistic regression (LR), occupancy models (OCC), and the Royle-Nichols abundance-induced heterogeneity estimator (RN). Simulations varied known detection functions of species (σ), and occurrence levels (ψ), and number of repeat visits (j).

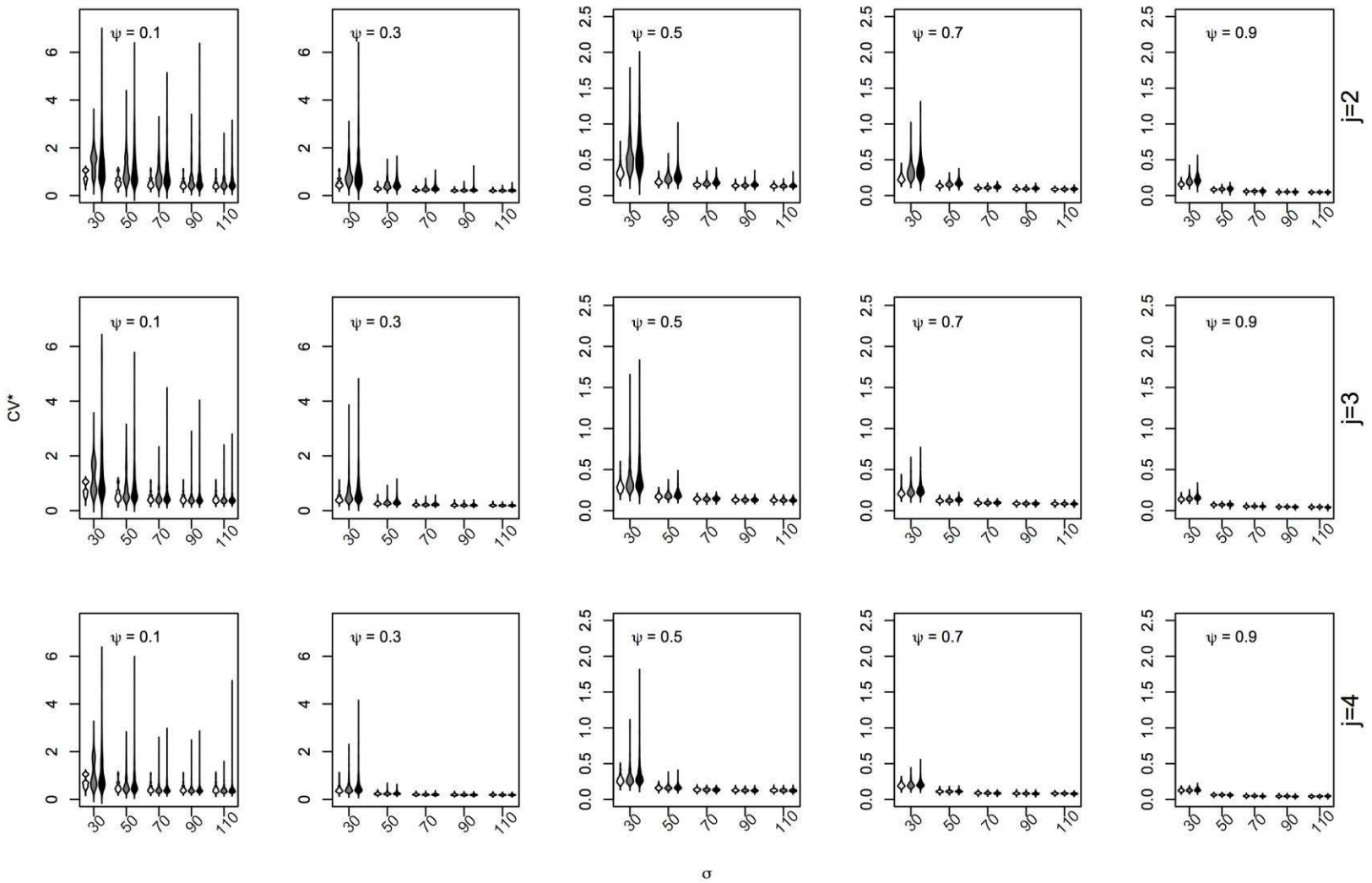

Figure 4.5. We derived a measure similar to coefficient of variation (CV*) by taking one fourth of the 95% CI (LR) or CR (OCC, RN) range divided by mean estimates. Density plots display CV* for each simulation by varying known occupancy (ψ), detection functions of individuals (σ), for 2-4 repeated surveys (j). Note that y-axes are not equal between ψ=0.1,0.3, and ψ=0.5, 0.7, 0.9.

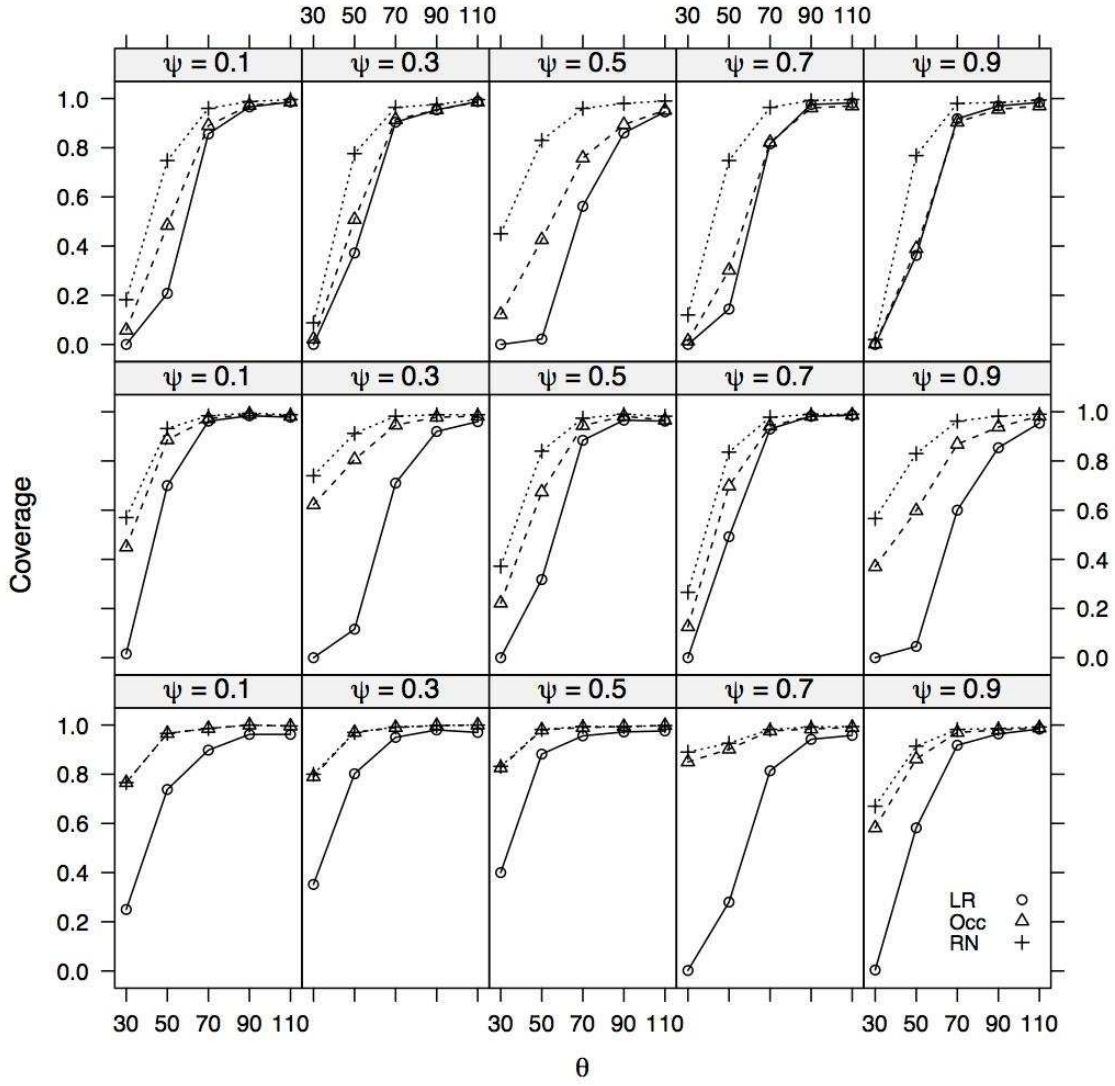

Figure 4.6. Coverage, calculated as proportion of simulations that contained the true parameter estimate within 95% CR (RN, OCC) or CI (LR). Top row includes simulations with j=2 surveys, followed by 3 and 4 surveys.

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Appendix 1.1. Model description of Bayesian gamma regression model with random effects used to estimate distribution for golden eagle productivity (average number of birds fledged per pair).

Posterior distribution for gamma regression model by fitting random effects for site (β_0) and year (β_1) to estimates of productivity ($\boldsymbol{y}$) from published literature.

$$\begin{aligned}\left[\alpha, \beta_0, \beta_1, \mu_{site}, \tau_{site}, \mu_{year}, \tau_{year} \mid \boldsymbol{y}\right] \propto & \left[\boldsymbol{y} \mid \alpha, \beta_0, \beta_1\right]\left[\beta_0 \mid \mu_{site}, \tau_{site}\right] \\ & \left[\beta_1 \mid \mu_{year}, \tau_{year}\right][\mu_{site}][\tau_{site}] \\ & [\mu_{year}][\tau_{year}][\alpha]\end{aligned}$$

Full model description with distributions placed on estimated and prior parameters.

$$y_i \sim \text{Gamma}(\alpha, \beta_i)$$

$$\alpha \sim \text{Uniform}(0, 100)$$

$$\beta_i = \frac{\alpha}{\exp(\pi_i)}$$

$$\pi_i = \beta_0[site_i] + \beta_1[year_i]$$

$$\beta_0 \sim \text{Normal}(\mu_{site}, \tau_{site})$$

$$\beta_1 \sim \text{Normal}\left(\mu_{year}, \tau_{year}\right)$$

$$\mu_{site} \sim \text{Normal}(0, 1000)$$

$$\tau_{site} \sim \text{Gamma}(0.001, 0.001)$$

$$\mu_{year} \sim \text{Normal}(0, 1000)$$

$$\tau_{year} \sim \text{Gamma}(0.001, 0.001)$$

We fit this gamma regression model to estimates of productivity using JAGS implemented in program R (Plummer 2012), using 3 chains each with 10,000 iterations following 2000 samples as burn-in. We visually inspected chains to assess convergence and that an adequate number of samples were run to estimate posterior distributions. We used shape

parameters for a gamma distribution describing productivity from the mean of posterior distribution estimates for shape parameters α and β.

Appendix 1.2. Sources of demographic vital rate estimates collated from published accounts for golden eagles and related species. Probability distributions fit to these data were subsequently used for the stochastic population models.

We reduced components of golden eagle life-history into productivity (P), 1st year survival (S_0), juvenile survival (S_j), non-breeding subadult and adult survival (S_{nb}), and breeding adult survival (S_b). When possible, we exclusively used estimates from western North American golden eagle (*Aquila chrysaetoes*; GOEA) populations; however, when data were sparse, we supplemented these estimates using data from Bonelli's eagles (*Aquila fasciata*; BOEA) and imperial eagles (*Aquila heliaca*; IMEA). Sample size (n) is reported if available in reports and publications.

Vital Rate	Species	Estimate	n	Year(s)	Region	Citation
P	GOEA	0.400	NA	1973	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.530	NA	1974	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.610	NA	1975	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.540	NA	1976	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.730	NA	1977	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.980	NA	1978	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.860	NA	1979	SRBPNCA	Steenhof et al. 1997
P	GOEA	1.180	NA	1980	SRBPNCA	Steenhof et al. 1997
P	GOEA	1.270	NA	1981	SRBPNCA	Steenhof et al. 1997
P	GOEA	1.380	NA	1982	SRBPNCA	Steenhof et al. 1997
P	GOEA	1.010	NA	1983	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.640	NA	1984	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.160	NA	1985	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.260	NA	1986	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.340	NA	1987	SRBPNCA	Steenhof et al. 1997

P	GOEA	0.590	NA	1988	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.690	NA	1989	SRBPNCA	Steenhof et al. 1997
P	GOEA	1.150	NA	1990	SRBPNCA	Steenhof et al. 1997
P	GOEA	1.060	NA	1991	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.830	NA	1992	SRBPNCA	Steenhof et al. 1997
P	GOEA	1.230	NA	1993	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.540	NA	1994	SRBPNCA	Steenhof et al. 1997
P	GOEA	0.680	30	2010	Livingston, Montana	Craighead Beringia South, 2014
P	GOEA	0.550	29	2011	Livingston, Montana	Craighead Beringia South, 2014
P	GOEA	0.510	27	2012	Livingston, Montana	Craighead Beringia South, 2014
P	GOEA	0.630	29	2013	Livingston, Montana	Craighead Beringia South, 2014
P	GOEA	0.630	29	2014	Livingston, Montana	Craighead Beringia South, 2014
P	GOEA	0.820	60	1988	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	1.210	58	1989	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.910	58	1990	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.890	62	1991	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.360	69	1992	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.390	72	1993	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.200	56	1994	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.430	56	1995	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.460	61	1996	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.840	69	1997	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.500	66	1998	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.960	72	1999	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.730	70	2000	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.460	68	2001	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.050	73	2002	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.270	71	2003	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.270	73	2004	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.500	76	2005	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.950	80	2006	Denali National Park	McIntyre and Schmidt 2012

P	GOEA	0.900	81	2007	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.690	75	2008	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.910	74	2009	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	0.650	75	2010	Denali National Park	McIntyre and Schmidt 2012
P	GOEA	1.500	NA	1975	Wyoming	Phillips and Beske 1990
P	GOEA	0.571	NA	1976	Wyoming	Phillips and Beske 1990
P	GOEA	0.700	NA	1977	Wyoming	Phillips and Beske 1990
P	GOEA	0.550	NA	1978	Wyoming	Phillips and Beske 1990
P	GOEA	0.750	NA	1979	Wyoming	Phillips and Beske 1990
P	GOEA	0.476	NA	1980	Wyoming	Phillips and Beske 1990
P	GOEA	1.083	NA	1981	Wyoming	Phillips and Beske 1990
P	GOEA	1.038	NA	1982	Wyoming	Phillips and Beske 1990
P	GOEA	1.250	NA	1983	Wyoming	Phillips and Beske 1990
P	GOEA	0.552	NA	1984	Wyoming	Phillips and Beske 1990
P	GOEA	0.367	NA	1985	Wyoming	Phillips and Beske 1990
P	GOEA	0.680	57	1996	Altamont Pass	Sinclair 1999
P	GOEA	0.590	59	1997	Altamont Pass	Sinclair 1999
P	GOEA	0.580	64	1998	Altamont Pass	Hunt 2002
P	GOEA	0.900	69	1999	Altamont Pass	Hunt 2002
P	GOEA	0.460	67	2000	Altamont Pass	Hunt 2002
S_0	GOEA	0.340*	22	1997 - 1997	Denali National Park	McIntyre et al. 2006
S_0	GOEA	0.190*	21	1999 - 1999	Denali National Park	McIntyre et al. 2006
S_0	GOEA	0.787	NA	1997 - 1997	Altamont Pass	Hunt and Hunt 2006
S_0	GOEA	0.840	NA	1997 - 2000	Altamont Pass	Hunt and Hunt 2006
S_0	GOEA	0.791	NA	1992 - 1992	Scotland	Whitfield et al. 2004
S_0	BOEA	0.780	NA	1990 - 1998	Spain	Carrete et al. 2005
S_0	IMEA	0.579	NA	1990 - 2001	Spain	Ortega et al. 2009
S_b	GOEA	0.909	NA	1997 - 2000	Altamont Pass	Hunt and Hunt 2006
S_b	BOEA	0.933	21	1980 - 1994	Burgos, Spain	Real and Mañosa 1997

S_b	BOEA	0.924	5	1984 - 1994	Navarra, Spain	Real and Mañosa 1997
S_b	BOEA	0.912	14	1980 - 1994	Valles, Spain	Real and Mañosa 1997
S_b	BOEA	0.871	46	1982 - 1994	Castello, Spain	Real and Mañosa 1997
S_b	BOEA	0.839	37	1983 - 1994	Murcia, Spain	Real and Mañosa 1997
S_b	BOEA	0.961	16	1982 - 1994	Provence, Spain	Real and Mañosa 1997
S_b	GOEA	0.959	NA	1992 - 1992	Scotland	Whitfield et al. 2004
S_b	GOEA	0.760	NA	1997 - 2001	Spain	Carrete et al. 2005
S_b	BOEA	0.890	NA	1990 - 1998	Spain	Carrete et al. 2005
S_b	IMEA	0.986	NA	1989 - 1993	Spain	Ortega et al. 2009
S_b	IMEA	0.918	NA	1994 - 1999	Spain	Ortega et al. 2009
S_b	IMEA	0.933	NA	2000 - 2004	Spain	Ortega et al. 2009
S_b	IMEA	0.840	NA	1998 - 2003	Kazakhstan	Rudnick et al. 2005
S_j	GOEA	0.787	NA	1997 - 1997	Altamont Pass	Hunt and Hunt 2006
S_j	GOEA	0.840	NA	1997 - 2000	Altamont Pass	Hunt and Hunt 2006
S_j	GOEA	0.791	NA	1992 - 1992	Scotland	Whitfield et al. 2004
S_j	GOEA	0.810	NA	1997 - 2001	Spain	Carrete et al. 2005
S_{nb}	GOEA	0.794	NA	1997 - 2000	Altamont Pass	Hunt and Hunt 2006
S_{nb}	GOEA	0.810	NA	1997 - 2001	Spain	Carrete et al. 2005
S_{nb}	GOEA	0.794	NA	1997 - 2000	Altamont Pass	Hunt and Hunt 2006
S_{nb}	GOEA	0.791	NA	1992 - 1992	Scotland	Whitfield et al. 2004
S_{nb}	GOEA	0.810	NA	1997 - 2001	Spain	Carrete et al. 2005
S_{nb}	GOEA	0.791	NA	1982 - 1982	Scotland	Whitfield et al. 2004
S_{nb}	GOEA	0.810	NA	1997 - 2001	Spain	Carrete et al. 2005

Snake River Birds of Prey National Conservation Area (SRBPNCA).
*Survival estimates from migratory populations were omitted in our efforts to recreate a non-migratory female-based population model. We assume that reproduction is similar between non-migratory and migratory individuals.

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Appendix 4.1. Full model selection results (Burnham and Anderson 2002) using logistic regression (LR), occupancy analyses (OCC), and the Royle and Nichols (RN; 2004) estimators. We fit all possible combinations of treatment (t); hyrdoaxing, chaining, and reference) or no effect (.) on parameters estimating occupancy (ψ) or detection (p). Note LR methods assume do not estimate detection.

Spp	Model	Structure	k	AICc 50m	dAICc 50m	AIC full	dAIC full
BGGN	RN	psi(.) p(.)	2	373.79	2.17	450.16	1.49
		psi(.) p(t)	4	371.62	0.00	450.09	1.42
		psi(t) p(.)	4	371.94	0.32	448.67	0.00
		psi(t) p(t)	5	374.79	3.17	452.20	3.53
	OCC	psi(.) p(.)	2	374.80	2.60	449.83	1.56
		psi(.) p(t)	4	372.50	0.30	449.36	1.09
		psi(t) p(.)	4	372.20	0.00	448.27	0.00
		psi(t) p(t)	5	375.70	3.50	451.84	3.57
	LR	psi(t)	3	170.16	7.18	173.48	4.55
		psi(.)	1	162.98	0.00	168.93	0.00
CHSP	RN	psi(.) p(.)	2	322.46	3.57	432.99	5.54
		psi(.) p(t)	4	318.89	0.00	427.55	0.10
		psi(t) p(.)	4	322.79	3.90	430.97	3.52
		psi(t) p(t)	5	321.59	2.70	427.45	0.00
	OCC	psi(.) p(.)	2	322.71	3.21	431.50	4.37
		psi(.) p(t)	4	319.50	0.00	427.13	0.00
		psi(t) p(.)	4	320.14	0.64	427.18	0.05
		psi(t) p(t)	5	322.41	2.91	427.83	0.70
	LR	psi(t)	3	167.40	0.00	168.50	1.58
		psi(.)	1	168.90	1.50	166.92	0.00
WBNU	RN	psi(.) p(.)	2	172.52	2.26	390.53	0.80
		psi(.) p(t)	4	170.26	0.00	390.70	0.97
		psi(t) p(.)	4	170.54	0.28	389.73	0.00
		psi(t) p(t)	5	174.25	3.99	392.77	3.04
	OCC	psi(.) p(.)	2	172.63	2.26	390.00	1.34
		psi(.) p(t)	4	170.37	0.00	389.81	1.15
		psi(t) p(.)	4	170.45	0.08	388.66	0.00
		psi(t) p(t)	5	174.36	3.99	392.38	3.72
	LR	psi(t)	3	117.54	0.78	173.48	2.16
		psi(.)	1	116.76	0.00	171.32	0.00

SPTO	RN	psi(.) p(.)	2	354.22	1.26	523.10	0.00
		psi(.) p(t)	4	352.96	0.00	523.35	0.25
		psi(t) p(.)	4	357.23	4.27	526.78	3.68
		psi(t) p(t)	5	354.71	1.75	527.31	4.21
	OCC	psi(.) p(.)	2	351.55	0.30	516.37	0.00
		psi(.) p(t)	4	351.25	0.00	516.73	0.36
		psi(t) p(.)	4	354.18	2.93	518.05	1.68
		psi(t) p(t)	5	352.86	1.61	520.67	4.30
	LR	psi(t)	3	165.61	0.00	139.77	0.00
		psi(.)	1	167.80	2.19	145.45	5.68
ROWR	RN	psi(.) p(.)	2	137.26	0.00	307.38	12.58
		psi(.) p(t)	4	137.92	0.66	294.80	0.00
		psi(t) p(.)	4	137.92	0.66	299.50	4.70
		psi(t) p(t)	5	140.78	3.52	298.36	3.56
	OCC	psi(.) p(.)	2	137.12	0.00	306.37	12.33
		psi(.) p(t)	4	137.76	0.64	294.04	0.00
		psi(t) p(.)	4	137.81	0.69	297.05	3.01
		psi(t) p(t)	5	140.71	3.59	297.73	3.69
	LR	psi(t)	3	104.41	0.00	160.19	5.88
		psi(.)	1	106.39	1.98	154.31	0.00